2.1.12. Herring Gull (gulls)

<u>Order *Charadriiformes*, Family *Laridae*</u>. Gulls are medium- to large-sized sea birds with long pointed wings, a stout, slightly hooked bill, and webbed feet. They are abundant in temperate coastal areas and throughout the Great Lakes. Although gulls may feed from garbage dumps and landfills, most take natural prey. Gulls nest primarily in colonies, although some of the larger species also nest solitarily. Many populations migrate annually between breeding and wintering areas. North American gull species range in size from Bonaparte's gull (33 cm bill tip to tail tip) to the great black-backed gull (76 cm).

Selected species

The herring gull (*Larus argentatus*) (64 cm) has the largest range of any North American gull, from Newfoundland south to the Chesapeake Bay along the north Atlantic and west throughout the Great Lakes into Alaska. Along the Pacific coast, the similar-sized western gull (*L. occidentalis*) is the ecological equivalent of the herring gull. Both species take primarily natural foods, especially fish, although some individuals of both species forage around fishing operations and landfills (Pierotti, 1981, 1987; Pierotti and Annett, 1987). The increase in number of herring gulls in this century has been attributed to the increasing abundance of year-round food supplies found in landfills (Drury, 1965; Harris, 1970); however, birds specializing on garbage have such low reproductive success that they cannot replace themselves in the population (Pierotti and Annett, 1987, 1991). An alternative explanation of the species' expansion is that cessation of taking of gulls by the feather industry in the late 1800's has allowed gull numbers to return to pre-exploitation levels (Graham, 1975).

***Body size*. Adult females (800 to 1,000 g) are significantly smaller than males (1,000 to 1,300 g) in both the herring gull (Greig et al., 1985) and the western gull (Pierotti, 1981). Chicks grow from their hatching weight of about 60 to 70 g to 800 to 900 g within 30 to 40 days, after which time their weight stabilizes (Dunn and Brisbin, 1980; Norstrom et al., 1986; Pierotti, 1982). Norstrom et al. (1986) fitted chick growth rates to the Gompertz equation as follows:**

$$BW = 997\ e^{-e(-0.088(t\ -\ 14.8))} \qquad \text{for females, and}$$

$$BW = 1193\ e^{-e(-0.075(t\ -\ 16.3))} \qquad \text{for males,}$$

where BW equals body weight in grams and t equals days after hatching. Adults show seasonal variation in body weight (Coulson et al., 1983; Norstrom et al., 1986).

***Habitat*. Nesting colonies of herring gulls along the northeastern coast of the United States are found primarily on sandy or rocky offshore or barrier beach islands (Kadlec and Drury, 1968). In the Great Lakes, they are found on the more remote, secluded, and protected islands and shorelines of the lakes and their connecting rivers (Weseloh, 1989). Smaller colonies or isolated pairs also can be found in coastal marshes (Burger, 1980a), peninsulas, or cliffs along seacoasts, lakes, and rivers (Weseloh, 1989), and occasionally in inland areas or on buildings or piers (Harris, 1964). Gulls are the most abundant seabirds**

offshore from fall through spring, and are only found predominantly inshore during the breeding season in late spring and summer (Powers, 1983; Pierotti, 1988). Gulls forage predominantly offshore, within 1 to 5 km of the coast (Pierotti, 1988). In all seasons the number of birds feeding at sea outnumber those feeding inshore (data from Powers, 1983; Pierotti, pers. comm.). Inshore, herring gulls forage primarily in intertidal zones but also search for food in wet fields, around lakes, bays, and rock jetties, and at landfills in some areas (Burger, 1988). In Florida, herring gull presence at landfills is restricted to the winter months (December through April) and may consist primarily of first-year birds that migrated from more northerly populations (e.g., from the Great Lakes) (Patton, 1988).

***Food habits*.** Gulls feed on a variety of foods depending on availability, including fish, squid, crustacea, molluscs, worms, insects, small mammals and birds, duck and gull eggs and chicks, and garbage (Bourget, 1973; Burger, 1979a; Fox et al., 1990; Pierotti and Annett, 1987). Gulls forage on open water by aerial dipping and shallow diving around concentrations of prey. At sea, such concentrations often are associated with whales or dolphins, other seabirds, or fishing boats (McCleery and Sibly, 1986; Pierotti, 1988). In the Great Lakes, concentrations of species such as alewife occur seasonally (e.g., when spawning) (Fox et al., 1990). Gulls also forage by stealing food from other birds and by scavenging around human refuse sites (e.g., garbage dumps, fish plants, docks, and seaside parks) (Burger and Gochfeld, 1981; 1983; Chapman and Parker, 1985). Individual pairs of gulls may specialize predominantly on a single type of food; for example, three quarters of a population of herring gulls in Newfoundland were found to specialize either on blue mussels, garbage, or adults of Leach's storm-petrel, with 60 percent of the specialists concentrating on mussels between 0.5 and 3 cm in length (Pierotti and Annett, 1987; 1991). Diet choices may change with the age and experience of adult birds as well as with availability of prey (Pierotti and Annett, 1987; 1991). Females take smaller prey and feed less on garbage than do males (Pierotti, 1981; Greig et al., 1985). For example, Fox et al. (1990) found females to feed more on smelt (100 to 250 mm) and males more on alewife (250 to 300 mm) in the Great Lakes region. Adult gulls sometimes attack and eat chicks of neighboring gulls or other species of seabird (Brown, 1967; Schoen and Morris, 1984). Juveniles up to 3 years of age forage less efficiently than adults (Greig et al., 1983; MacLean, 1986; Verbeek, 1977). In the Great Lakes, herring gulls' high consumption of alewife during their spawn may result in high exposures of the gulls to lipophilic contaminants that biomagnify (Fox et al., 1990).

***Metabolism*.** Norstrom et al. (1986) have estimated an annual energy budget for free-living female herring gulls that breed in the Great Lakes and an annual energy budget for free-living juvenile herring gulls in the Great Lakes in their first year. Between September and March, the nonbreeding season, they estimate that adult females require 250 to 260 kcal/day. Following a dip in energy requirements to 210 kcal/day when the male feeds the female during courtship, the female's needs increase to peak at 280 kcal/day for egg production, then fall to approximately 210 kcal/day during incubation. The energy required to forage for food for the chicks is substantial, rising through July to peak in August at 310 to 320 kcal/day, then declining again until September when feeding chicks has ceased. These estimates compare well with those derived from Nagy's (1987) equation to estimate free-living metabolic rates for seabirds, except that the energy peaks required to produce eggs and to feed chicks are not included in Nagy's model. Readers interested in the metabolic rates of first-year herring gulls are referred to Norstrom et al. (1986). Ellis

(1984) provides an overview of seabird energetics and additional discussion of approaches and models for estimating metabolic rates of free-ranging seabirds.

***Molt*.** Gull chicks are downy gray with dark brown spotting and molt into a dark-gray or brown mottled juvenile plumage. At the end of the first year, portions of the plumage have paled, and by the second year, gray plumage develops along the back and top of wings. By their third year, young gulls resemble dirty adults, and they acquire their full adult plumage by 4 years (Harrison, 1983; Kadlec and Drury, 1968). Adult gulls, at least in some populations, begin their primary feather molt during incubation and complete the molt by mid- to late fall (Coulson et al., 1983). They molt and replace the large body feathers from mid-summer to early fall (Coulson et al., 1983).

***Migration*.** Herring gull populations along the northeast coast of North America tend to be migratory, while adult herring gulls of the Great Lakes are year-round residents. Along the western North Atlantic, most herring gulls arrive on their breeding grounds between late February and late April. They remain until late August or early September when they leave for their wintering grounds along the Atlantic and Gulf coasts or well offshore (Burger, 1982; Pierotti, 1988). Adult and older subadult herring gulls in the Great Lakes area are essentially nonmigratory (Mineau et al., 1984; Weseloh et al., 1990). Thus, in contrast to other fish-eating birds in the Great Lakes system that migrate south in the winter, herring gulls are exposed to any contaminants that may be in Great Lakes' fish throughout the year (Mineau et al., 1984). Postbreeding dispersal away from breeding colonies begins in late July and ends in August, with all ages traveling short distances. Great Lakes herring gulls less than a year old usually migrate to the Gulf or Atlantic coast (Smith, 1959; Mineau et al., 1984), traveling along river systems and the coast (Moore, 1976).

***Breeding activities and social organization*.** Gulls nest primarily in colonies on offshore islands, and nest density is strongly affected by population size (Pierotti, 1981; 1982; 1987). Typically, males arrive at the breeding grounds first and establish territories. Both sexes build the nest of vegetation on the ground in areas that are sheltered from wind but may be exposed to the sun (Pierotti, 1981; 1982). Males feed females for 10 to 15 days prior to the start of egg laying (Pierotti, 1981). From the laying of the first egg until the chicks are 3 to 4 weeks old, one or both parents will be present at all times (Tinbergen, 1960). Males perform most territorial defense, females perform most incubation, and both parents feed the chicks until they are at least 6 to 7 weeks old (Burger, 1981; Pierotti, 1981; Tinbergen, 1960). All gulls are strongly monogamous; pair bonds can persist for 10 or more years and usually only are terminated by the death of a mate or failure to reproduce successfully (Tinbergen, 1960). Males may be promiscuous in populations with more females than males (Pierotti, 1981). Herring gull colonies often are found in association with colonies of other species, including other gulls (Bourget, 1973; Brown, 1967). In some nesting colonies, gulls attack chicks of neighboring gulls and other species (Brown, 1967; Schoen and Morris, 1984).

***Home range and resources*.** During the breeding season, herring gulls defend a territory of several tens of square meters around the immediate vicinity of the nest (Burger, 1980b). Their daily foraging range depends on the availability of prey and on the foraging strategy, age, and sex of the gull. Using radiotelemetry on gulls in the Great Lakes, Morris and Black (1980) demonstrated that some parents with chicks forage at specific locations within 1 km of the colony whereas other parents make extended flights to destinations across a lake more than 30 km away. Similarly, gulls that feed at sea may range tens of kilometers from their nest whereas gulls from the same colony feeding in the intertidal zone may travel less than 1 km (Pierotti and Annett, 1987; 1991). Males typically range farther than females and take larger prey items (Pierotti and Annett, 1987; 1991). At sea during the nonbreeding season, gulls may range hundreds of kilometers during a day (Pierotti, pers. comm.).

***Population density*.** As described above, population density is determined by available nesting space, size of the breeding population, and quality of habitat. Small islands with good feeding areas nearby can have several hundred nests per hectare (Kadlec, 1971; Parsons, 1976b; Pierotti, 1982). In poor quality habitat, some pairs nest solitarily without another nest for several kilometers (Weseloh, 1989).

***Population dynamics*.** Herring gulls and western gulls usually do not begin breeding until at least 4 years of age for males and 5 years of age for females (Burger, 1988; Pierotti, 1981; Pierotti, pers. comm.). Kadlec and Drury (1968) suggest that in a given year, 15 to 30 percent of adults of breeding age do not breed. Most breeding females produce three-egg clutches, but individuals in poor condition may lay only one or two eggs (Parsons, 1976a; Pierotti, 1982; Pierotti and Annett, 1987; 1991). Herring gulls will lay replacement eggs if all or a portion of their original clutch is destroyed (Parsons, 1976a). Hatching success appears to be influenced by female diet, with garbage specialists hatching a smaller percentage of eggs than fish or intertidal (mussel) specialists (Pierotti and Annett, 1987, 1990, 1991). Predation, often by gulls of the same or other species, also contributes to egg losses (Paynter, 1949; Harris, 1964; Davis, 1975). Many herring gull chicks that hatch die before fledging, most within the first 5 days after hatching (Harris, 1964; Kadlec et al., 1969; Brown, 1967). Adult mortality is low (around 10 percent per year), and some birds may live up to 20 years (Brown, 1967; Kadlec and Drury, 1968). Subadult birds exhibit higher mortality (20 to 30 percent per year) (Kadlec and Drury, 1968; Chabrzyk and Coulson, 1976).

Similar species (from general references)

- **The western gull (*Larus occidentalis*) (64 cm), found on the Pacific coast of the United States, is the ecological equivalent of the herring gull and is similar in size (53 cm); males range from 1,000 to 1,300 g and females from 800 to 1,000 g (Pierotti, 1981).**

- **The glaucous gull (*Larus hyperboreus*) is larger (69 cm) than the herring gull and is the predominant gull breeding in the high arctic. Birds from Alaska are slightly smaller than birds from eastern Canada.**

- **The glaucous-winged gull (*Larus glaucescens*) is similar in size to the herring gull (66 cm) and is the primary breeding species north of the Columbia River. This species hybridizes extensively with the herring gull in Alaska.**

- **The California gull (*Larus californicus*) is smaller (53 cm) than the herring gull. This species breeds primarily in the Great Basin Desert and winters along the Pacific coast.**

- **The great black-backed gull (*Larus marinus*) is the largest species of gull (76 cm) in North America and breeds from Labrador to Long Island.**

- **The ring-billed gull (*Larus delawarensis*) is of average size (45 cm) and is the most common breeding gull in the Great Lakes and northern prairies.**

- **Franklin's gull (*Larus pipixcan*) is a small (37 cm), summer resident of the Great Plains.**

General references

For general information: Harrison (1983); National Geographic Society (1987); Tinbergen (1960); Graham (1975). For discussion of diet: Burger (1988); Fox et al. (1990); Pierotti (1981); Pierotti and Annett (1987).

Herring Gull (*Larus argentatus*)

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A F spring A M spring	951 ± 88 SD 1,184 ± 116 SD		Lake Huron	Norstrom et al., 1986	
	A F summer A M summer	999 ± 90 SD 1,232 ± 107 SD	832 - 1,274 1,014 - 1,618	Newfoundland	Threlfall & Jewer, 1978	
	at hatching 10 days old 20 days old 30 days old	65 230 590 810	50 - 80 120 - 380 420 - 800 610 - 1,000	Maine	Dunn & Brisbin, 1980	
	30 days old 30 days old	964 ± 77 SD 818 ± 99 SD		Newfoundland/rocky island Newfoundland/grassy island	Pierotti, 1982	1
Chick Growth Rate (g/day)	< 5 days 5-30 days	8.8 - 13.1 26.3 ± 6.5 SD		Newfoundland/island Newfoundland/island meadow	Pierotti, 1982 Pierotti, 1982	
	5-30 days	33.4 ± 4.7 SD		Newfoundland/rocky island	Pierotti, 1982	
	5-25 days	30.2 ± 1.75 SD	26.7 - 31.4	Maine/coastal island	Hunt, 1972	
Egg Weight (g)	3 egg clutch 2 egg clutch	87.2 85.7		New Brunswick	Herbert & Barclay, 1988	
	in 1983 in 1984	92.0 ± 5.9 SD 98.0 ± 8.0 SD		Lake Superior, Canada	Meathrel et al., 1987	
Metabolic Rate (kcal/kg-day)	A M basal A F basal	86 91			estimated	2
	A standard	99		laboratory	Lustick et al., 1978	
	A M free-living A F free-living	233 248	(84 - 646) (92 - 669)		estimated	3
	Also see text for a discussion of annual variation in free-living metabolic rate in herring gulls.					

Herring Gull (*Larus argentatus*)

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-day)	A M breeding A F breeding	0.20 0.21		Newfoundland - diet of mussels	Pierotti & Annett, 1991	4
	A M breeding A F breeding	0.19 0.18		Newfoundland - diet of garbage	Pierotti & Annett, 1991	5
Water Ingestion Rate (g/g-day)	A M A F	0.055 0.059			estimated	6
Inhalation Rate (m^3/day)	A M A F	0.48 0.41			estimated	7
Surface Area (cm^2)	A M A F	1,150 1,001			estimated	8

Dietary Composition	Summer	Summer	Summer	Summer	Location/Habitat (measure)	Reference	Note No.
months:	Mid-May/ Mid-June	Mid-June/ Mid-July	Mid-July/ Mid-Aug.		Newfoundland/island	Haycock & Threlfall, 1975	
Mytilus edulis	30.9	0.9	9.1		(% occurrence in regurgitations and pellets)		
sea urchin	5.8	0.0	4.5				
fish	11.4	71.1	18.9				
Oceanodroma leuchorhoa	22.4	7.0	15.9				
Fratercula arctica adults	5.8	0.0	1.5				
Fratercula, Uria chicks	0.0	3.5	9.1				
Larus sp. eggs	3.1	0.9	0.8				
Vaccinum angustifolium	-	-	9.9				
Gadus morhua offal	12.4	1.7	14.4				
assorted refuse	5.8	0.9	6.8				

Herring Gull (*Larus argentatus*)

Dietary Composition	Summer	Summer	Summer	Summer	Location/Habitat (measure)	Reference	Note No.
year:	1978	1979	1980	1981	Lake Ontario	Fox et al., 1990	
American smelt	46.1	18.4	61.2	57.8			
alewife	23.1	73.7	16.7	23.4	(% occurrence in		
other fish	20.5	0	3.4	3.1	regurgitations from and		
birds	2.6	2.6	13.8	6.2	stomach contents of		
voles	2.6	2.6	3.4	9.4	incubating adults)		
insects & refuse	12.8	0	3.4	0			
lake:	Ontario	Erie	Huron	Superior	Great Lakes	Fox et al., 1990	
fish	91.8	94.1	75.8	38.6			
insects	5.5	5.9	5.6	42.1	(% occurrence in boli		
offal, garbage	0.5	2.9	13.6	21.0	regurgitated by chicks)		
gull chicks	2.2	0	1.0	0			
adult birds	1.6	0	1.0	3.5			
amphibians	0.5	0	0	0			
earthworms	2.2	0	11.6	1.7			
crayfish	0	0	0.5	0			
snails		3			CA,FL,NY,NJ,TX/	Burger, 1988	
crabs		14			coastal		
garbage		27					
offal		5			(% of gulls feeding on items)		
worms		23					
other inverts.		28			offshore feeding on fish was		
fish		unknown			not included in observations		

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Foraging Radius (km)	A M A F	10 to 15 5 to 10	3 - 50 3 - 25	NS/coastal	Pierotti, pers. comm.	
Population Density (nests/ha)	summer	227	138 - 350	Massachusetts/coastal islands	Kadlec, 1971	
	summer	217 75		Newfoundland/island - rocky Newfoundland/island - grassy slope	Pierotti, 1982 Pierotti, 1982	

Herring Gull (*Larus argentatus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Clutch Size		2.78	2.51 - 2.90 (over 8 sites)	New Jersey/salt marsh islands	Burger, 1979b	
		2.54	1 - 6 (per nest)	NE United States/coastal	Nisbet & Drury, 1984	
		2.38	2.3 - 2.8 (over 11 years)	Maine/coastal islands	Hunt, 1972	
		2.84 ± 0.44 SD		Lake Superior, Canada/ islands	Meathrel et al., 1987	
Clutches/Year		1	1 - 2*	(* if first eggs lost)	Burger, 1979a; Bourget, 1973	
Days Incubation		30.5	28 - 33	Holland/NS	Tinbergen, 1960	
		29		Newfoundland/island	Pierotti, 1982	9
Age at Fledging (days)		51	35 - 44 to 56 - 61	Massachusetts/coastal island	Kadlec et al., 1969	
		43	31 to 52	New Brunswick/island	Paynter, 1949	
Number Fledge per Active Nest	3 colonies	1.42	1.40 - 1.44	New Jersey/coastal	Burger & Shisler, 1980	
	6 colony-yrs	1.65	1.40 - 2.13	Lake Ontario/lakeshore	Mineau et al., 1984 (minimum and maximum are yearly means)	
	3 colony-yrs	1.78	1.62 - 2.10	Lake Erie/lakeshore		
	6 colony-yrs	2.19	2.16 - 2.25	Lake Huron/lakeshore		
Number Fledge per Successful Nest	3 colonies	1.80	1.79 - 1.80	New Jersey/coastal	Burger & Shisler, 1980	
Age at Sexual Maturity	F	5 years		throughout range/NS	Greig et al., 1983; Pierotti, pers. comm.	
	M	4 - 5 years				
	B	4.3 to 5.8	3 - 8	Scotland/coastal	Coulson et al., 1982	
Annual Mortality Rates (percent)	A B	8		New England/coastal	Kadlec & Drury, 1968	
	J B	22	17 - 33			
	A B	7.3		Scotland/coastal	Chabryzk & Coulson, 1976	

Herring Gull (*Larus argentatus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Longevity	A B	10	up to 30 years	NS/NS	Pierotti, pers. comm.	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/ Laying	late April	early May	early June	ne shore Lake Superior	Morris & Haymes, 1977	
	early May	mid-May	early June	Maine	Bourget, 1973	
	early May	mid-May	mid-June	New Jersey	Burger, 1977, 1979b	
	early May	late May	end May	Newfoundland	Pierotti, 1982	
Hatching		mid - late May		Great Lakes	Fox et al., 1990	
	May	June	July	Massachusetts	Kadlec, 1971	
	early June	mid-June	end June	Newfoundland	Pierotti, 1982, 1987	
	late June	late June	mid-July	New Brunswick	Paynter, 1949	
Migration spring	February		late April	northwestern Atlantic populations	Burger, 1982	
fall	August		September			
Molt	June	July	August	Newfoundland	Pierotti, pers. comm.	

1 Weight of chicks from first egg laid in 1978 for the rocky island and in 1977 for the grassy area. In some years and some locations, chicks from the first egg were heavier than the rest, and at other times and locations, the first chick was lighter.
2 Estimated using equation 3-29 (Lasiewski and Dawson, 1967) and body weights from Threlfall and Jewer (1978).
3 Estimated using equation 3-38 (Nagy, 1987) and body weights from Threlfall and Jewer (1978).
4 Estimated using 11.2 meals of mussel consumed per day per pair, weight of 80 g per mussel meal of which half is shell and not included in ingestion rate, assuming that the female accounts for 46 percent of pair's energy requirement and the male accounts for 54 percent, and using the body weights of Threlfall and Jewer (1978).
5 Estimated using 4.2 meals of garbage consumed per day per pair, weight of 100 g per garbage meal, assuming that the female accounts for 46 percent of pair's energy requirement and the male accounts for 54 percent, and using the body weights of Threlfall and Jewer (1978).
6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Threlfall and Jewer (1978).
7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Threlfall and Jewer (1978).
8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Threlfall and Jewer (1978).
9 Beginning with first egg.

References (including Appendix)

Belopol'skii, L. O. (1957) (Ecology of sea colony birds of the Barents Sea). Translated by: Israel Program for Scientific Translations, Jerusalem (cited in Dunning, 1984).

Bourget, A. A. (1973) Relation of eiders and gulls nesting in mixed colonies in Penobscot Bay, Maine. Auk 90: 809-820.

Brown, R. G. (1967) Breeding success and population growth in a colony of herring gulls and lesser black-backed gulls *Larus argentatus* and *L. fuscus*. Ibis 109: 502-515.

Burger, J. (1977) Nesting behavior of herring gulls: invasion into *Spartina* salt marsh areas of New Jersey. Condor 79: 162-169.

Burger, J. (1979a) Competition and predation: herring gulls versus laughing gulls. Condor 81: 269-277.

Burger, J. (1979b) Colony size: a test for breeding synchrony in herring gull (*Larus argentatus*) colonies. Auk 96: 694-703.

Burger, J. (1980a) Nesting adaptation of herring gull (*Larus argentatus*) to salt marshes and storm tides. Biol. Behav. 5: 147-162.

Burger, J. (1980b) Territory size differences in relation to reproductive stage and type of intruder in herring gulls (*Larus argentatus*). Auk 97: 733-741.

Burger, J. (1981) On becoming independent in herring gulls: parent-young conflict. Am. Nat. 117: 444-456.

Burger, J. (1982) Herring gull. In: Davis, D. E., ed. CRC handbook of census methods for terrestrial vertebrates. Boca Raton, FL: CRC Press; pp. 76-79.

Burger, J. (1988) Foraging behavior in gulls: differences in method, prey, and habitat. Colonial Waterbirds 11: 9-23.

Burger, J.; Gochfeld, M. (1981) Age-related differences in piracy behavior of four species of gulls, *Larus*. Behaviour 77: 242-267.

Burger, J.; Gochfeld, M. (1983) Behavior of nine avian species at a Florida garbage dump. Colonial Waterbirds 6: 54-63.

Burger, J.; Shisler, J. (1980) The process of colony formation among herring gulls *Larus argentatus* nesting in New Jersey. Ibis 122: 15-16.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Chabrzyk, G.; Coulson, J. C. (1976) Survival and recruitment in the herring gull *Larus argentatus*. J. Anim. Ecol. 45: 187-203.

Chapman, B.-A.; Parker, J. W. (1985) Foraging areas, techniques, and schedules of wintering gulls on southeastern Lake Erie. Colonial Waterbirds 8: 135-141.

Coulson, J. C.; Duncan, N.; Thomas, C. (1982) Changes in the breeding biology of the herring gull (*Larus argentus*) induced by reduction in size and density of the colony. J. Anim. Ecol. 51: 739-756.

Coulson, J. C.; Monaghan, P.; Butterfield, J.; et al. (1983) Seasonal changes in the herring gull in Britain: weight, moult and mortality. Ardea 71: 235-244.

Davis, J. W. (1975) Age, egg-size and breeding success in the herring gull *Larus argentatus*. Ibis 117: 460-473.

Drury, W. H., Jr. (1965) Clash of coastal nesters. MA: Audubon.

Dunn, E. H. (1976) The development of endothermy and existence energy expenditure in herring gull chicks. Condor 78: 493-498.

Dunn, E. H. (1980) On the variability in energy allocation of nestling birds. Auk 1: 19-27.

Dunn, E. H.; Brisbin, I. L. (1980) Age-specific changes in the major body components and caloric values of herring gull chicks. Condor 82: 398-401.

Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.

Ellis, H. I. (1984) Energetics of free-ranging seabirds. In: Whittow, G. C.; Rhan, H., eds. Seabird energetics. New York, NY: Plenum Press; pp. 203-234.

Erwin, R. M. (1971) The breeding success of two species of sympatric gulls, the herring gull and the great black-backed gull. Wilson Bull. 83: 152-158.

Ewins, P. J.; Weseloh, D. V.; Groom, J. H.; et al. (unpublished 1991) The diet of herring gulls (*Larus argentatus*) during winter and early spring on the lower Great Lakes (unpublished manuscript, Canadian Wildlife Service, Burlington, Ontario).

Fox, G. A.; Allan, L. J.; Weseloh, D. V., et al. (1990) The diet of herring gulls during the nesting period in Canadian waters of the Great Lakes. Can. J. Zool. 68: 1075-1085.

Graham, F. (1975) Gulls: a social history. New York, NY: Random House.

Greig, S. A.; Coulson, J. C.; Monaghan, P. (1983) Age-related differences in foraging success in the herring gull (*Larus argentatus*). Anim. Behav. 31: 1237-1243.

Greig, S. A.; Coulson, J. C.; Monaghan, P. (1985) Feeding strategies of male and female adult herring gulls *Larus argentatus*. Behaviour 94: 41-59.

Gross, A. O. (1940) The migration of Kent Island herring gulls. Bird-Banding 11: 129-155.

Harris, M. P. (1964) Aspects of the breeding biology of the gulls: *Larus argentatus*, *L. fuscus*, and *L. marinus*. Ibis 106: 432-456.

Harris, M. P. (1970) Rates and causes of increases of some British gull populations. Bird Study 17: 325-335.

Harrison, P. (1983) Seabirds: an identification guide. Boston, MA: Houghton-Mifflin Co.

Haycock, K. A.; Threlfall, W. (1975) The breeding biology of the herring gull in Newfoundland. Auk 92: 678-697.

Hebert, P. N.; Barclay, R. M. (1986) Asynchronous and synchronous hatching: effect on early growth and survivorship of herring gull, *Larus argentatus*, chicks. Can. J. Zool. 64: 2357-2362.

Hebert, P. N.; Barclay, R. M. (1988) Parental investment in herring gulls: clutch apportionment and chick survival. Condor 90: 332-338.

Holley, A. J. (1982) Post-fledging interactions on the territory between parents and young herring gulls *Larus argentatus*. Ibis 124: 198-203.

Hunt, G. L. (1972) Influence of food distribution and human disturbance on the reproductive success of herring gulls. Ecology 53: 1051-1061.

Kadlec, J. A. (1971) Effects of introducing foxes and raccoons on herring gull colonies. J. Wildl. Manage. 35: 625-636.

Kadlec, J. A. (1976) A re-evaluation of mortality rates in adult herring gulls. Bird-Banding 47: 8-12.

Kadlec, J. A.; Drury, W. H. (1968) Structure of the New England herring gull population. Ecology 49: 644-676.

Kadlec, J. A.; Drury, W. H.; Onion, D. K. (1969) Growth and mortality of herring gull chicks. Bird-Banding 40: 222-233.

Keith, J. A. (1966) Reproduction in a population of herring gulls (*Larus argentatus*) contaminated by DDT. J. Appl. Ecol. 3(suppl.): 57-70.

Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.

Lasiewski, R. C.; Dawson, W. R. (1967) A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.

Lustick, S.; Battersby, B.; Kelty, M. (1978) Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200: 81-83.

Lustick, S.; Battersby, B.; Kelty, M. (1979) Effects of insolation on juvenile herring gull energetics and behavior. Ecology 60: 673-678.

MacLean, A. A. (1986) Age-specific foraging ability and the evolution of deferred breeding in three species of gulls. Wilson Bull. 98: 267-279.

McCleery, R. H.; Sibley, R. M. (1986) Feeding specialization and preference in herring gulls. J. Anim. Ecol. 55: 245-259.

Meathrel, C. E.; Ryder, J. P.; Termaat, B. M. (1987) Size and composition of herring gull eggs: relationship to position in the laying sequence and the body condition of females. Colonial Waterbirds 10: 55-63.

Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.

Mendall, H. L. (1939) Food habits of the herring gull in relation to freshwater game fishes in Maine. Wilson Bull. 41: 223-226.

Mineau, P.; Fox, G. A.; Norstrom, R. J.; et al. (1984) Using the herring gull to monitor levels and effects of organochlorine contamination in the Canadian Great Lakes. In: Nriagu, J. O.; Simmons, M. S., eds. Toxic contaminants in the Great Lakes. New York, NY: John Wiley & Sons; pp. 425-452.

Moore, F. R. (1976) The dynamics of seasonal distribution of Great Lakes herring gulls. Bird-Banding 47: 141-159.

Morris, R. D.; Black, J. E. (1980) Radiotelemetry and herring gull foraging patterns. J. Field Ornithol. 51: 110-118.

Morris, R. D.; Haymes, G. T. (1977) The breeding biology of two Lake Erie herring gull colonies. Can. J. Zool. 55: 796-805.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.

Niebuhr, V. (1983) Feeding strategies and incubation behavior of wild herring gulls: an experiment using operant feeding boxes. Anim. Behav. 31: 708-717.

Nisbet, I. C.; Drury, W. H. (1984) Super-normal clutches in herring gulls in New England. Condor 86: 87-89.

Norstrom, R. J.; Clark, T. P.; Kearney, J. P.; et al. (1986) Herring gull energy requirements and body constituents in the Great Lakes. Ardea 74: 1-23.

Olsson, V. (1958) Dispersal, migration, longevity and death causes of *Strix aluco*, *Buteo buteo*, *Ardea cinerea* and *Larus argentatus*. A study based on recoveries of birds ringed in Fenno-Scandia. Acta Vertebratica 1: 91-189.

Parsons, J. (1972) Egg size, laying date and incubation period in the herring gull. Ibis 114: 536-541.

Parsons, J. (1976a) Factors determining the number and size of eggs laid by the herring gull. Condor 78: 481-482.

Parsons, J. (1976b) Nesting density and breeding success in the herring gull *Larus argentatus*. Ibis 118: 537-546.

Patton, S. R. (1988) Abundance of gulls at Tampa Bay landfills. Wilson Bull. 100: 431-442.

Paynter, R. A. (1949) Clutch size and the egg and chick mortality of Kent Island herring gulls. Ecology 30: 146-166.

Pierotti, R. (1981) Male and female parental roles in the western gull under different environmental conditions. Auk 98: 532-549.

Pierotti, R. (1982) Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. Ecology 63: 854-868.

Pierotti, R. (1987) Behavioral consequences of habitat selection in the herring gull. Studies Avian Biol. 10: 119-128.

Pierotti, R. (1988) Associations between marine birds and mammals in the northwest Atlantic Ocean. In: Burger, J., ed. Seabirds and other marine vertebrates. New York, NY: Columbia University Press; pp. 31-58.

Pierotti, R.; Annett, C. (1987) Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil, A. C.; Krebs, J.; Pulliam, H. R., eds. Foraging behavior. New York, NY: Plenum Press; pp. 417-442.

Pierotti, R.; Annett, C. A. (1990) Diet and reproductive output in seabirds: food choices by individual, free-living animals can affect survival of offspring. BioSci. 40: 568-574.

Pierotti, R.; Annett, C. A. (1991) Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. Ecology 72: 319-328.

Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.

Powers, K. D. (1983) Pelagic distributions of marine birds off the northeastern U.S. NOAA, Tech. Mem. NMFS-F/NED-27: 1-201.

Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.

Schoen, R. B.; Morris, R. D. (1984) Nest spacing, colony location, and breeding success in herring gulls. Wilson Bull. 96: 483-488.

Sibly, R. M.; McCleery, R. H. (1983) Increase in weight of herring gulls while feeding. J. Anim. Ecol. 52: 35-50.

Smith, W. J. (1959) Movements of Michigan herring gulls. Bird-Banding 30: 69-104.

Threlfall, W.; Jewer, D. D. (1978) Notes on the standard body measurements of two populations of herring gulls (*Larus argentatus*). Auk 95: 749-753.

Tinbergen, N. (1960) The herring gull's world. New York, NY: Harper and Row, Publishers.

Verbeek, N. A. (1977) Comparative feeding behavior of immature and adult herring gulls. Wilson Bull. 89: 415-421.

Vermeer, K. (1973) Food habits and breeding range of herring gulls in the Canadian prairie provinces. Condor 75: 478-480.

Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

Weseloh, D. H. (1989) Herring gull. In: Cadman, M. D.; Eagles, P. F.; Helleiner, F. M., eds. Atlas of the breeding birds of Ontario. Waterloo, University of Waterloo Press; pp. 182-183.

Weseloh, D. V.; Mineau, P.; Struger, J. (1990) Geographical distribution of contaminants and productivity measures of herring gulls in the Great Lakes: Lake Erie and connecting channels 1978/79. Sci. Tot. Environ. 91: 141-159.

2.1.13. Belted Kingfisher (kingfishers)

Order *Coraciiformes*, Family *Alcedinidae*. Kingfishers are stocky, short-legged birds with large heads and bills. They exist on a diet mostly of fish, which they catch by diving, from a perch or the air, head first into the water. They nest in burrows in earthen banks that they dig using their bills and feet.

Selected species

The belted kingfisher (*Ceryle alcyon*, formerly *Megaceryle alcyon*) is a medium-sized bird (33 cm bill tip to tail tip) that eats primarily fish. It is one of the few species of fish-eating birds found throughout inland areas as well as coastal areas. The belted kingfisher's range includes most of the North American continent; it breeds from northern Alaska and central Labrador southward to the southern border of the United States (Bent, 1940). Two subspecies sometimes are recognized: the eastern belted kingfisher (*Ceryle alcyon alcyon*), which occupies the range east of the Rocky Mountains and north to Quebec, and the western belted kingfisher (*Cercyle alcyon caurina*), which occupies the remaining range to the west (Bent, 1940).

***Body size*. The sexes are similar in size and appearance, although the female tends to be slightly larger (Salyer and Lagler, 1946). Bent (1940) reported that western populations are somewhat larger than eastern ones. Nestlings reach adult body weight by about 16 days after hatching, but then may lose some weight before fledging (Hamas, 1981).**

***Habitat*. Belted kingfishers are typically found along rivers and streams and along lake and pond edges (Hamas, 1974). They are also common on seacoasts and estuaries (Bent, 1940). They prefer waters that are free of thick vegetation that obscures the view of the water and water that is not completely overshadowed by trees (Bent, 1940; White, 1953). Kingfishers also require relatively clear water in order to see their prey and are noticeably absent in areas when waters become turbid (Bent, 1940; Davis, 1982; Salyer and Lagler, 1946). White (1953) suggested that water less than 60 cm deep is preferred. They prefer stream riffles for foraging sites even when pools are more plentiful because of the concentration of fish at riffle edges (Davis, 1982). Belted kingfishers nest in burrows within steep earthen banks devoid of vegetation beside rivers, streams, ponds, and lakes; they also have been found to nest in slopes created by human excavations such as roadcuts and landfills (Hamas, 1974). Sandy soil banks, which are easy to excavate and provide good drainage, are preferred (Brooks and Davis, 1987; Cornwell, 1963; White, 1953). In general, kingfishers nest near suitable fishing areas when possible but will nest away from water and feed in bodies of water other than the one closest to home (Cornwell, 1963).**

***Food habits*. Belted kingfishers generally feed on fish that swim near the surface or in shallow water (Salyer and Lagler, 1946; White, 1953; Cornwell, 1963). Davis (pers. comm. in Prose, 1985) believes that these kingfishers generally catch fish only in the upper 12 to 15 cm of the water column. Belted kingfishers capture fish by diving either from a perch overhanging the water or after hovering above the water (Bent, 1940). Fish**

are swallowed whole, head first, after being beaten on a perch (Bent, 1940). The average length of fish caught in a Michigan study was less than 7.6 cm but ranged from 2.5 to 17.8 cm (Salyer and Lagler, 1946); Davis (1982) found fish caught in Ohio streams to range from 4 to 14 cm in length. Several studies indicate that belted kingfishers usually catch the prey that are most available (White, 1937, 1953; Salyer and Lagler, 1946; Davis, 1982). Diet therefore varies considerably among different water bodies and with season (see examples in Appendix). Although kingfishers feed predominantly on fish, they also sometimes consume large numbers of crayfish (Davis, 1982; Sayler and Lagler, 1946), and in shortages of their preferred foods, have been known to consume crabs, mussels, lizards, frogs, toads, small snakes, turtles, insects, salamanders, newts, young birds, mice, and berries (Bent, 1940). Parents bring surprisingly large fish to their young. White (1953) found that nestlings only 7 to 10 days old were provided fish up to 10 cm long, and nestlings only 2 weeks old were provided with fish up to 13 cm in length. After fledging, young belted kingfishers fed on flying insects for their first 4 days after leaving the nest, crayfish for the next week, and by the 18th day post-fledging, could catch fish (Salyer and Lagler, 1946).

***Molt*.** The juvenile plumage is maintained through the winter, and young birds undergo their first prenuptial molt in the spring (between February and April) involving most of the body plumage (Bent, 1940). Adults have a complete postnuptial molt in the fall (August to October) (Bent, 1940).

***Migration*.** This kingfisher breeds over most of the area of North America and winters in most regions of the continental United States (National Geographic Society, 1987). Although most northern kingfishers migrate to southern regions during the coldest months, some may stay in areas that remain ice-free where fishing is possible (Bent, 1940).

***Breeding activities and social organization*.** During the breeding season, pairs establish territories for nesting and fishing (Davis, 1982); otherwise, belted kingfishers are solitary. They are not colonial nesters and will defend an unused bank if it lies within their territory (Davis, 1982). In migrating populations, the males arrive before the females to find suitable nesting territories (Davis, 1982). Kingfishers excavate their burrows in earthen banks, forming a tunnel that averages 1 to 2 m in length, although some burrows may be as long as 3 to 4 m (Hamas, 1981; Prose, 1985). The burrow entrance is usually 30 to 90 cm from the top of the bank (Bent, 1940; White, 1953) and at least 1.5 m from the base (Cornwell, 1963). Burrows closer to the top may collapse, and burrows too low may flood (Brooks and Davis, 1987). Burrows may be used for more than one season (Bent, 1940). Five to seven eggs are laid on bare substrate or on fish bones within the burrow (Hamas, 1981; White, 1953). Only one adult, usually the female, spends the night in the nest cavity; males usually roost in nearby forested areas or heavy cover (Cornwell, 1963). Both parents incubate eggs and feed the young (Bent, 1940). After fledging, the young remain with their parents for 10 to 15 days (Sayler and Lagler, 1946).

***Home range and resources*.** During the breeding season, belted kingfishers require suitable nesting sites with adequate nearby fishing. During spring and early summer, both male and female belted kingfishers defend a territory that includes both their nest site and their foraging area (Davis, 1982). By autumn, each bird (including the young of the year)

defends an individual feeding territory only (Davis, 1982). The breeding territories (length of waterline protected) can be more than twice as long as the fall and winter feeding territories, and stream territories tend to be longer than those on lakes (Davis, 1982; Salyer and Lagler, 1946). Foraging territory size is inversely related to prey abundance (Davis, 1982).

***Population density*. Breeding densities of between two and six pairs per 10 km of river shoreline have been recorded, with density increasing with food availability (Brooks and Davis, 1987; White, 1936).**

***Population dynamics*. Kingfishers are sensitive to disturbance and usually do not nest in areas near human activity (White, 1953; Cornwell, 1963). Kingfishers typically breed in the first season after they are born (Bent, 1940). Fledging success depends on food availability, storms, floods, predation, and the integrity of the nest burrow but can be as high as 97 percent (M. J. Hamas, pers. comm.). Dispersal of young occurs within a month of fledging (White, 1953). No data concerning annual survivorship rates were found.**

Similar species (from general references)

- **The green kingfisher (*Chloroceryle americana*) is smaller (22 cm) than the belted kingfisher and is only common in the lower Rio Grande Valley. It also is found in southeastern Arizona and along the Texas coast, usually during fall and winter.**

- **The ringed kingfisher (*Ceryle torquata*) is larger (41 cm) and resides in the lower Rio Grande Valley in Texas and Mexico.**

General references

Bent (1940); Fry (1980); National Geographic Society (1987); Prose (1985); White (1953).

Belted Kingfisher (*Ceryle alcyon*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	A B	148 ± 20.8 SD	125 - 215	Pennsylvania	Powdermill Nature Center (unpubl.)	1
	A B	136 ± 15.6 SE		Pennsylvania	Brooks & Davis, 1987	
	A B	158 ± 11.5 SE		Ohio	Brooks & Davis, 1987	
	at hatching	10 - 12		Minnesota	Hamas, 1981	
	at fledging	148 ± 13.3 SE		Pennsylvania	Brooks & Davis, 1987	
	at fledging	169 ± 11.9 SE		Ohio	Brooks & Davis, 1987	
Nestling Growth Rate (g/day)		5 to 6		Pennsylvania, Ohio/streams	Brooks & Davis, 1987	2
Metabolic Rate (kcal/kg-day)	A B basal	132			estimated	3
	A B free-living	327	(154 - 693)		estimated	4
Food Ingestion Rate (g/g-day)	A B	0.50		northcentral lower Michigan	Alexander, 1977	5
	nestlings		1.0 - 1.75	Nova Scotia	White, 1936	
Water Ingestion Rate (g/g-day)	A B	0.11			estimated	6
Inhalation Rate (m^3/day)	A B	0.094			estimated	7
Surface Area (cm^2)	A B	280			estimated	8

Belted Kingfisher (*Ceryle alcyon*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
trout non-trout fish crustacea insects amphibians birds and mammals unidentified		17* 29 5 19 27 1 2			lower Michigan/lake (% wet weight; stomach contents) *data from spring and fall also	Alexander, 1977	
trout other game & pan fish (e.g., perch, centrarchids) forage fish (e.g., minnow, stickleback, sculpins) unidentified fish crayfish insects		30 13 15 1 41 < 1			Michigan/trout streams (% wet volume; stomach contents)	Salyer & Lagler, 1946	
salmon fry salmon (1-yr-old) salmon (2-yr-old) trout sticklebacks killifish suckers		11 42 1 15 30 < 1 < 1			Nova Scotia/riparian - streams (% of total number of prey; fecal pellets)	White, 1936	
crayfish cyprinids (minnows) (stonerollers) (unidentified) other fish		13 76 (13) (38) (26) 10			southwest Ohio/creek (% of total number of prey brought to nestlings)	Davis, 1982	

Belted Kingfisher (*Ceryle alcyon*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory Size (km shoreline)	early summer - breeding pairs:	2.19 ± 0.56 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		1.03 ± 0.28 SE		Ohio/streams	Brooks & Davis, 1987	
	late summer - nonbreeding individuals:	1.03 ± 0.22 SE		southwest Ohio/streams	Davis, 1980	
		0.39 ± 0.093 SE		southwest Ohio/streams	Davis, 1980	
Population Density (pair/km shore)	A B summer	0.11 - 0.19		Pennsylvania/streams	Brooks & Davis, 1987	
	A B summer	0.6		Nova Scotia/streams	White, 1936	
Clutch Size		5.8 ± 0.7 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		6.8 ± 0.4 SE		Ohio/streams	Brooks & Davis, 1987	
Clutches/Year		1		Pennsylvania, Ohio/streams	Brooks & Davis, 1987	9
		1		Minnesota/lake	Hamas, 1975	
Days Incubation		22		Minnesota/lake	Hamas, 1975	
Age at Fledging		28 days		NS/NS	Bent, 1940	
Number Fledge per Active Nest		4.5 ± 1.9 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		5.3 ± 2.2 SE		Ohio/streams	Brooks & Davis, 1987	
Age at Sexual Maturity		1 year		throughout range	Bent, 1940	

Belted Kingfisher (*Ceryle alcyon*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	April	April to May	early July	Minnesota	Hamas, 1975	
Hatching	May	June early June	late July	Minnesota Nova Scotia	Hamas, 1975 White, 1936	
Molt fall spring	August February		October April	NS NS	Bent, 1940 Bent, 1940	
Migration fall departures			mid-October mid-November mid-December	Maine NY, SD, WI, NE Massachusetts, New Jersey	Bent, 1940 Bent, 1940 Bent, 1940	
spring arrivals	late February mid-March early April			PA, RI, MO NY, CT, IL, WI Maine, Nova Scotia	Bent, 1940 Bent, 1940 Bent, 1940	

1 Cited in Dunning (1984).
2 Brooks and Davis (1987) reported fledging weights of 149 and 169 g for two populations. Given a hatching weight of about 10 g and 28 days required to fledge, on average, chicks must gain 5 to 6 g per day. Hamas (1981) found gains of approximately 8.5 g per day until day 18, and a loss of approximately 4.5 g per day until fledging.
3 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Powdermill Nature Center (unpubl.).
4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Powdermill Nature Center (unpubl.).
5 Estimated by author.
6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Powdermill Nature Center (unpubl.).
7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Powdermill Nature Center (unpubl.).
8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Powdermill Nature Center (unpubl.).
9 They are known to renest up to three times if clutches are lost early (Bent, 1940).

References (including Appendix)

Alexander, G. R. (1974) The consumption of trout by bird and mammal predators on the North Branch Au Sable River. Michigan Dept. Nat. Resources, Dingell - Johnson Proj.; F-30-R, Final Report.

Alexander, G. R. (1977) Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10: 181-195.

Bent, A. C. (1940) Life histories of North American cuckoos, goat suckers, hummingbirds, and their allies. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. US Nat. Mus., Bull. 176.

Brooks, R. P.; Davis, W. J. (1987) Habitat selection by breeding belted kingfishers (*Ceryle alcyon*). Am. Midl. Nat. 117: 63-70.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Cornwell, G. W. (1963) Observations on the breeding biology and behavior of a nesting population of belted kingfishers. Condor 65: 426-431.

Davis, W. J. (1980) The belted kingfisher, *Megaceryle alcyon*: its ecology and territoriality [master's thesis]. Cincinnati, OH: University of Cincinnati.

Davis, W. J. (1982) Territory size in *Megaceryle alcyon* along a stream habitat. Auk 99: 353-362.

Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.

Fry, C. (1980) The evolutionary biology of kingfishers (*Alcedinidae*). In: The living bird, 1979-80. Ithaca, NY: The Laboratory of Ornithology, Cornell University; pp. 113-160.

Hamas, M. J. (1974) Human incursion and nesting sites of the belted kingfisher. Auk 91: 835-836.

Hamas, M. J. (1975) Ecological and physiological adaptations for breeding in the belted kingfisher (*Megaceryle alcyon*) [Ph.D. dissertation]. Duluth, MN: University of Minnesota.

Hamas, M. J. (1981) Thermoregulatory development in the belted kingfisher. Comp. Biochem. Physiol. A: Comp. Physiol. 69: 149-152.

Lasiewski, R. C.; Calder, W. A. (1971) A preliminary allometric analysis of respiratory variables in resting birds. Resp. Phys. 11: 152-166.

Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.

Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.

Poole, E. L. (1938) Weights and wing areas in North American birds. Auk 55: 511-517.

Prose, B. L. (1985) Habitat suitability index models: belted kingfisher. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.87).

Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.

Salyer, J. C.; Lagler, K. F. (1946) The eastern belted kingfisher, *Megaceryle alcyon alcyon* (Linnaeus), in relation to fish management. Trans. Am. Fish. Soc. 76: 97-117.

Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

White, H. C. (1936) The food of kingfishers and mergansers on the Margaree River, Nova Scotia. J. Biol. Board Can. 2: 299-309.

White, H. C. (1937) Local feeding of kingfishers and mergansers. J. Biol. Board Can. 3: 323-338.

White, H. C. (1938) The feeding of kingfishers: food of nestlings and effect of water height. J. Biol. Board 4: 48-52.

White, H. C. (1953) The eastern belted kingfisher in the maritime provinces. Fish. Res. Board Can. Bull. 97.

2.1.14. Marsh Wren (wrens)

<u>Order *Passeriformes*, Family *Troglodytidae*</u>. Wrens are small insectivorous birds that live in a variety of habitats throughout the United States. They have long, slender bills adapted for gleaning insects from the ground and vegetation. Most species are migratory, although some populations are year-round residents.

Selected species

The marsh wren (*Cistothorus palustris*) is a common bird inhabiting freshwater cattail marshes and salt marshes. Marsh wrens breed throughout most of the northern half of the United States and in coastal areas as far south as Florida; they winter in the southern United States and into Mexico, particularly in coastal areas. Marsh wrens eat mostly insects, and occasionally snails, which they glean from the surface of vegetation. This species was formerly known as the long-billed marsh wren (*Telmatodytes palustris*).

***Body size*. Although wrens are small (13 cm bill tip to tail tip; about 10 g body weight), males tend to be about 10 percent heavier than females (see table). Body weight varies seasonally; in Georgia, where marsh wrens are resident throughout the year, they tend to be heavier in the spring and summer than in the fall and winter (Kale, 1965).**

***Habitat*. Marsh wrens inhabit freshwater and saltwater marshes, usually nesting in association with bulrushes, cattails, and sedges or on occasion in mangroves (Welter, 1935; Bent, 1948; Kale, 1965; Verner, 1965). Standing water from several centimeters to nearly a meter is typical of the areas selected (Bent, 1948). Permanent water is necessary to provide a food supply of insects necessary to maintain the birds and as a defense against predation (Verner and Engelsen, 1970). Deeper water and denser vegetation are associated with reduced predation rates (Leonard and Picman, 1987).**

***Food habits*. Marsh wrens consume aquatic invertebrates, other insects, and spiders, which they glean from the water surface, on stems and leaves of emergent vegetation, and the marsh floor (Kale, 1965; Welter, 1935). They sometimes also feed by flycatching (Welter, 1935). The insect orders most commonly taken include Coleoptera (both adults and larvae), Diptera (adults and larvae), Hemiptera (juveniles and adults), Lepidoptera (larvae most commonly fed to nestlings); and Odonata (newly emerged) (Bent, 1948; Kale, 1964). When feeding the young, at first the parents bring mosquito adults and larvae, midges, larval tipulids, and other small insects (Welter, 1935). As the young mature, the parents bring larger insects such as ground beetles, diving beetles, long-horned beetles, caterpillars, dragonflies, and sawflies to the nestlings (Welter, 1935). In a population in Georgia, spiders (usually 1 to 3 mm in size, sometimes 12 to 15 mm), small crabs (5 to 7 mm), small snails (1 to 3 mm), and insect eggs also were consumed and fed to nestlings (Kale, 1965). Thus, organisms that are aquatic for all or part of their lives are an important component of the diet of marsh wren adults and nestlings.**

***Migration*. Marsh wrens are year-round residents in some southern and coastal maritime regions where marshes do not freeze. Most migratory wrens breed throughout the northern half of the United States through southern Canada and winter in Mexico and**

the southern half of the United States (Bent, 1948; Verner, 1965; American Ornthologists' Union, 1983; National Geographic Society, 1987).

Breeding activities and social organization. **Many populations of marsh wren are polygynous, with some males mating with two, occasionally three, females in a season, while the remaining males have one mate or remain bachelors. For example, Leonard and Picman (1987) found 5 to 11 percent bachelor males, 41 to 48 percent monogamous males, 37 to 43 percent bigamous males, and 5 to 12 percent trigamous males in two marshes in Manitoba, Canada. Similarly, Verner and Engelsen (1970) found 16 percent bachelors, 57 percent monogamous, and 25 percent bigamous males in eastern Washington state. In contrast, Kale (1965) found most males to be monogamous through 4 years of study in Georgia.**

Males arrive at the breeding marshes before the females to establish territories that include both nest sites and foraging areas (Kale, 1965; Verner, 1965; Welter, 1935). Males build several nests in their territories throughout the breeding season (Kale, 1965; Verner, 1965). The female usually only adds lining material to a nest of her choice, although some may help construct the breeding nest (Kale, 1965). Breeding nests are oblong in shape, with a side opening, and are woven of cattails, reeds, and grasses and lashed to standing vegetation, generally 30 cm to 1 m above standing water or high tide (Bent, 1948; Verner, 1965). Incubation lasts approximately 2 weeks, as does the nestling period (Kale, 1965; Verner, 1965). After fledging, one or both parents continue to feed the young for about 12 days (Verner, 1965). Many populations typically rear two broods per year, although some may rear three (Kale, 1965; Verner, 1965). In the more monogamous populations, both parents regularly feed young, but in the more polygynous ones, the females may provide most of the food, with males assisting only toward the end of the nestling period (Leonard and Picman, 1988; Verner, 1965).

Home range and resources**. Marshes smaller than 0.40 ha usually are not used by breeding marsh wrens (Bent, 1948). Average male territory size for a given year and location can range from 0.006 to 0.17 ha, depending on the habitat and conditions of the year (see table). Also, there is a trend in polygynous populations for polygynous males to defend larger territories than monogamous males or males that end up as bachelors (Verner and Engelson, 1970; Verner, 1964; Kale, 1965).**

Population density**. Because the species is polygynous, there may be more females than males inhabiting breeding marshes. Population density varies with the suitability and patchiness of the habitat. Densities as high as 120 adult birds per hectare have been recorded (Kale, 1965).**

Population dynamics**. Clutch size and number of clutches per year vary with latitude and climate (see table). In some populations, marsh wrens commonly destroy eggs and kill the nestlings of other pairs of their own species and other marsh-nesting passerines (Orians and Wilson, 1964; Picman, 1977; Welter, 1935). Fledging success depends strongly on nest location; nests over deeper water are less vulnerable to predation (Leonard and Picman, 1987). Of nests lost to all causes, Leonard and Picman (1987) found 44 percent due to mammalian predators, 27 percent due to other wrens, 11 percent due to weather, 8 percent due to nest abandonment, and 13 percent unknown. The**

annual mortality of adults is lower than that of first-year birds. Both sexes of this species usually commence breeding in the first year following hatching (Kale, 1965).

Similar species

- **The sedge wren (*Cistothorus platensis*, formerly known as the short-billed marsh wren) nests locally in wet meadows or shallow sedge marshes and hayfields in the northeastern United States, wintering primarily in the southeastern United States. It is slightly smaller (11 cm) than the marsh wren.**

  Note: None of the other wren species inhabit marshes, although all forage by gleaning insects from vegetation and other surfaces. Wrens that inhabit moist woodlands and open areas are listed below.

- **The house wren (*Troglodytes aedon*) (12 cm) breeds throughout most of the United States, into southern Canada. It inhabits open habitats with brush and shrubs and is found in orchards, farmyards, and urban gardens and parks.**

- **The winter wren (*Troglodytes troglodytes*) (10 cm) breeds in southern Canada, where it nests in dense brush, especially along moist coniferous woodlands. It winters primarily in the southeastern United States, where it inhabits many types of woodlands.**

- **The Carolina wren (*Thryothorus ludovicianus*) (14 cm) is nonmigratory and can be found in both summer and winter in the eastern United States as far north as northern Delaware and as far west as Oklahoma. It inhabits moist woodlands and swamps and wooded suburban areas.**

- **Bewick's wren (*Thryomanes bewickii*) (13 cm) is more common in western States than the house wren and is declining east of the Mississippi. It is found in brushland, stream edges, and open woods.**

General references

Kale (1965); Gutzwiller and Anderson (1987); Leonard and Picman (1987); Verner (1965), National Geographic Society (1987).

Marsh Wren (*Cistothorus palustris)*

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	F breeding	10.6 ± 0.99 SD	9.0 - 13.5	New York	Tintle (unpubl.)	1
	M breeding	11.9 ± 0.72 SD	10.5 - 13.5			
	A F	9.4 ± 1.1 SD		Georgia	Kale, 1965	2
	A M	10.6 ± 0.7 SD				
	J B	9.4 ± 1.6 SD				
	nestling:			New York, Minnesota/fresh marshes	Welter, 1935	3
	day 1	1.1				
	day 3	2.1				
	day 5	4.7				
	day 7	6.8				
	day 9	10.0				
	day 11	10.6				
	day 13	11.3				
	at fledging	8.84 ± 0.70 SD		Georgia	Kale, 1965	
Egg Weight (g)		1.14 ± 0.10 SD		Georgia	Kale, 1965	
Metabolic Rate (lO_2/kg-day)	A B basal	91.2		Georgia (captive)	Kale, 1965	4
	A B near basal	113				5
	A B light activity	169				6
Metabolic Rate (kcal/kg-day)	A B basal	444		Georgia (captive)	Kale, 1965	7
	A B near basal	557 ± 115 SD			Kale, 1965	8
	A B light activity	788 ± 115 SD			Kale, 1965	9
		880 ± 90 SD			Kale, 1965	10
	A B free-living					
		1,209	(571 - 2,563)		estimated	11
	A F free-living	1,174	(554 - 2,486)			
	A M free-living					

Marsh Wren (*Cistothorus palustris)*

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Food Ingestion Rate	A B free-living	1,155 ± 130 SD kcal/kg-day		Georgia (captive)	Kale, 1965	12
	A B free-living	0.67 g/g-day		Georgia (captive)	estimated from Kale, 1965	13
	A F free-living A M free-living	0.99 g/g-day 0.96 g/g-day			estimated	14
Water Ingestion Rate (g/g-day)	A F A M	0.28 0.26			estimated	15
Surface Area (cm^2)	A F A M	45 48			estimated	16

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
Hymenoptera		17.3		12.4	Georgia/salt marsh	Kale, 1965	17
Homoptera		13.0		40.1			
Coleoptera		11.6		12.6	(% wet volume; stomach contents)		
Lepidoptera		14.6		2.9			
Diptera		8.9		7.7			
Hemiptera		5.4		10.0			
Orthoptera		5.6		0.8			
spiders		15.1		6.2			
other arthropods (crabs, amphipods)		1.8		0.9			
molluscs (snails)		3.5		4.0			
other (insect eggs, undetermined, etc.)		4.5		3.3			

Marsh Wren (*Cistothorus palustris)*

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory Size (ha)	A M spring	0.0060 ± 0.0014 SD 0.0156 ± 0.0050 SD 0.0085 ± 0.0042 SD		Georgia/salt marsh 1, 1958 Georgia/salt marsh 2, 1958 Georgia/salt marsh 2, 1959	Kale, 1965	
	A M spring	0.17 ± 0.021 SE	0.0242 - 0.360	west Washington/fresh mixed-species marsh	Verner, 1965	
	A M spring	0.07 ± 0.06 SD		Manitoba/fresh cattail marsh	Leonard & Picman, 1986	
Population Density	spring: pairs/ha	48.3 ± 5.3 SD	45.1 - 56.2	Georgia/salt marsh (4 years)	Kale, 1965	
	males/ha	8.5 16.9		west Washington/fresh mixed-species marsh (2 areas)	Verner, 1965	
	males/ha	3.7 ± 0.5 SD	3.4 - 4.3	Manitoba/fresh mixed-species marsh (3 years)	Leonard & Picman, 1987	
Clutch Size		4.5	3 - 5	Georgia/salt marsh	Kale, 1965	
		6.0 ± 0.19 SD	4 - 8	east Washington/fresh pond-margin marsh	Verner, 1965	
		5.8 ± 0.8 SD		Manitoba/fresh cattail marsh	Leonard & Picman, 1987	
Clutches/Year		1 - 2	0 - 3	Georgia/salt marsh	Kale, 1965	
		2	0 - 2	east Washington/fresh pond- margin marsh	Verner, 1965	
		2 - 3	0 - 3	west Washington/fresh mixed-species marsh	Verner, 1965	
Days Incubation		13.1	12 - 14	Georgia/salt marsh	Kale, 1965	
		15.1	13 - 16	west Washington/fresh marsh	Verner, 1965	

Marsh Wren (*Cistothorus palustris*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Age at Fledging	B B	12 - 13 14	10 - 15 11 - 16	Georgia/salt marsh Washington/fresh marshes	Kale, 1965 Verner, 1965	
Number Fledge per Active Nest		3.4 ± 3.4 SD		Manitoba/fresh mixed marsh	Leonard & Picman, 1987	
Number Fledge per Successful Nest		4.5 ± 1.3 SD 5.1 ± 1.2 SD		Manitoba/fresh mixed-species marsh Manitoba/fresh cattail marsh	Leonard & Picman, 1987 Leonard & Picman, 1987	
Age at Sexual Maturity	B B	1 year 1 year		Manitoba/fresh marsh Washington/fresh marsh	Leonard & Picman, 1987 Verner, 1971	
Annual Mortality Rates (percent)	A B J B	32 70		Georgia/salt marsh	Kale, 1965	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	April mid-April late March late May	 May - June April - May	mid-August early July mid-July early August	Georgia eastern Washington (Turnbull) western Washington (Seattle) New York	Kale, 1965 Verner, 1965 Verner, 1965 Welter, 1935	
Hatching	early May mid-April		mid-July early August	eastern Washington (Turnbull) western Washington (Seattle)	Verner, 1965 Verner, 1965	
Migration fall	September		late October	New York, Minnesota	Welter, 1935	
spring	April	May mid-March (nonmigratory)	June	New York, Minnesota eastern Washington (Turnbull) western Washington (Seattle)	Welter, 1935 Verner, 1965 Verner, 1965	

Marsh Wren (*Cistothorus palustris)*

1 As cited in Dunning (1984).

2 Collection dates not specified. Resident population; presumably averaged from birds captured throughout the year.

3 Estimated from Welter's (1935) growth curve based on 50 nestlings.

4 Measured by oxygen respirometry; lowest value of metabolism of postabsorptive wrens resting in the dark (but not at night) at temperatures within the thermoneutral zone.

5 Measured by oxygen respirometry; birds not postabsorptive, but resting in a dark box at temperatures within the thermoneutral zone.

6 Measured by oxygen respirometry; birds somewhat active in their cage.

7 Estimated from oxygen consumption, for conditions, see note 3.

8 Estimated from oxygen consumption, for conditions, see note 4.

9 Estimated from oxygen consumption, for conditions, see note 5.

10 Estimated from measured daily food intake, excretory losses, assimilation, and respiration for active birds in small cages (173 weekly determinations total). Because of the birds' high activity levels, Kale (1965) considered the measure representative of free-living birds.

11 Estimated using allometric equation 3-36 (Nagy, 1987) and body weights from Kale (1965).

12 Measured daily food intake of birds in cages and measured caloric content of diet provided. Because of the birds' high activity levels, Kale (1965) considered the measure representative of free-living birds.

13 Estimated from Kale's (1965) measured daily food intake (see note 11) assuming 5.62 kcal/gram (dry weight) insects, a 70 percent assimilation efficiency, and a 67 percent water content for insects.

14 Estimated from free-living metabolic rate estimated from Nagy's (1987) equation 3-36 (see note 10) assuming the same parameters described in note 12. These predicted food ingestion rates (>0.95 g/g-day) for free-living birds exceed the value estimated for Kale's (1965) caged birds (0.67 g/g-day); however, the latter does not include metabolic requirements of searching for food, reproduction, or unusual thermoregulatory demands.

15 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Kale (1965).

16 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Kale (1965).

17 Summer column represents combination of spring and summer data; winter column represents combination of fall and winter data.

References (including Appendix)

American Ornithologists' Union. (1983) Check-list of North American birds. Lawrence, KS: Allen Press, Inc.

Bent, A. C. (1948) Life histories of North American nuthatches, wrens, thrashers, and their allies. Washington, DC: U.S. Government Printing Office; Smithsonian Inst. U.S. Nat. Mus., Bull. 195.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.

Gutzwiller, K. J.; Anderson, S. H. (1987) Habitat suitability index models: marsh wren. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.139).

Kale, H. W., II (1964) Food of the long-billed marsh wren, *Telmatodytes palustris griseus*, in the salt marshes of Sapelo Island, Georgia. Oriole 29: 47-61.

Kale, H. W., II. (1965) Ecology and bioenergetics of the long-billed marsh wren *Telmatoidytes palustris griseus* (Brewster) in Georgia salt marshes. Publ. Nuttall Ornith. Club No. 5.

Leonard, M. L.; Picman, J. (1986) Why are nesting marsh wrens and yellow-headed blackbirds spatially segregated? Auk 103: 135-140.

Leonard, M. L.; Picman, J. (1987) Nesting mortality and habitat selection by marsh wrens. Auk 104: 491-495.

Leonard, M. L.; Picman, J. (1988) Mate choice by marsh wrens: the influence of male and territory quality. Anim. Behav. 36: 517-528.

Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.

Orians, G. H.; Wilson, M. F. (1964) Interspecific territories of birds. Ecology 45: 736-745.

Picman, J. (1977) Intraspecific nest destruction in the long-billed marsh wren, *Telmatodytes palustris plustris*. Can. J. Zool. 55: 1997-2003.

Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.

Verner, J. (1964) Evolution of polygamy in the long-billed marsh wren. Evolution 18: 252-261.

Verner, J. (1965) Breeding biology of the long-billed marsh wren. Condor 67: 6-30.

Verner, J. (1971) Survival and dispersal of male long-billed marsh wrens. Bird-Banding 42: 92-98.

Verner, J.; Engelsen, G. H. (1970) Territories, multiple nest building, and polygamy in the long-billed marsh wren. Auk 87: 557-567.

Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

Welter, W. A. (1935) The natural history of the long-billed marsh wren. Wilson Bull. 47: 3-34.

2.1.15. American Robin (thrushes)

<u>Order *Passeriformes*, Family *Muscicapidae*, Subfamily *Turdinae*</u>. Thrushes are common, medium-sized birds that eat worms, insects, and fruit. They live in a variety of habitats, including woodlands, swamps, suburbs, and parks. Most thrushes build nests of mud and vegetation on the ground or in the crotches of trees or shrubs; bluebirds nest in holes in trees and posts or in nest boxes. This group forages primarily on the ground and in low vegetation by probing and gleaning. Some thrushes are neotropical migrants while others reside year-round in North America. Thrushes range in size from the eastern and western bluebirds (18 cm from bill tip to tail tip) to the American robin (25 cm). Male and female plumages are similar in most thrushes, although in some species, such as the bluebirds, the males are more brightly colored.

Selected species

The American robin (*Turdus migratorius*) occurs throughout most of the continental United States and Canada during the breeding season and winters in the southern half of the United States and in Mexico and Central America. The breeding range of the robin has expanded in recent times with the increasing area covered by lawns and other open habitats (Howell, 1942; Martin et al., 1951; James and Shugart, 1974).

***Body size*. The sexes are similar in size and appearance. Their size varies slightly geographically; the smallest robins are found in the eastern United States and along the Pacific coast, and the largest ones occur in the Rocky Mountains, northern Great Plains, and northern deserts (Aldrich and James, 1991).[d] The size of robins tends to increase with latitude in eastern North America but does not in western North America (Aldrich and James, 1991). Fledglings attain adult size at approximately 6 weeks of age (Howell, 1942).**

***Habitat*. Access to fresh water, protected nesting sites, and productive foraging areas are important requirements for breeding robins (Speirs, 1953). Breeding habitats include moist forests, swamps, open woodlands, orchards, parks, and lawns. Robins forage on the ground in open areas, along habitat edges, or the edges of streams; they also forage above ground in shrubs and within the lower branches of trees (Paszkowski, 1982; Malmborg and Willson, 1988). Nests in wooded areas are usually near some type of opening such as the forest edge or a treefall gap (Young, 1955; Knupp et. al., 1977). During the nonbreeding season, robins prefer moist woods or fruit-bearing trees and shrubs (Robbins et al., 1983). In the fall, flocks of migratory robins are often found along forest edges or clearings where fruits are most plentiful (Baird, 1980).**

***Food habits*. Robins forage by hopping along the ground in search of ground-dwelling invertebrates and by searching for fruit and foliage-dwelling insects in shrubs and low tree branches (Malmborg and Willson, 1988; Paszkowski, 1982). In the months preceding and during the breeding season, robins feed mainly (greater than 90 percent volume) on invertebrates and on some fruits; during the remainder of the year, their diet**

---

[d]Based on linear measurements of museum study skins.

consists primarily (over 80 to 99 percent by volume) of fruits (Martin et al., 1951; Gochfeld and Burger, 1984; Wheelwright, 1986). Robins eat a wide variety of both plant and animal foods; in a compilation of diet records collected throughout the United States and southern Canada, Wheelwright (1986) found that robins consumed fruits from 51 genera and invertebrates from 107 families. Commonly eaten fruits include plums, dogwood, summac, hackberries, blackberries, cherries, greenbriers, raspberries, and juniper (Martin et al., 1951; Wheelwright, 1986); common invertebrates include beetles, caterpillars, moths, grasshoppers, spiders, millipedes, and earthworms (Martin et al., 1951; Wheelwright, 1986; Paszkowski, 1982). Wheelwright (1986) has compiled seasonal changes in the proportion of plants and invertebrates consumed by robins in three different sections of the United States (see table). Wheelwright (1986) also has summarized the average occurrence of fruits of various plant families in the stomachs of robins by month for these sections. Martin et al. (1951) have summarized the occurrence of fruits of various plant families in more specific areas of the United States (see Appendix).

Wheelwright (1986) found no differences between the sexes in the proportion or types of invertebrates and fruits eaten. Very young robins (up to at least 35 days of age) feed almost entirely on insects and other invertebrates (Howell, 1940). Older juveniles tend to eat a higher proportion of fruit and easy-to-capture prey than adults (Gochfeld and Burger, 1984; Wheelwright, 1986). In a given area, robins often show food preferences: a population in central New York seemed to prefer northern arrowwood and spice bush fruits over most other plants (Wheelwright, 1988); in Illinois, a group ate predominantly frost grapes and Virginia creeper in the late summer and fall (Malmborg and Willson, 1988).

During seasons when fruits dominate the diet, robins may need to consume quantities in excess of their body weight to meet their metabolic needs each day (see table). Robins as well as other fruit-eating birds exhibit a low digestive efficiency for fruits; Karasov and Levey (1990) estimated the metabolizable energy coefficient (MEC) (i.e., the proportion of food energy that actually is assimilated) for robins eating a mixed fruit diet to be only 55 percent, perhaps because of the low retention time of the digested matter in the gut (Levey and Karasov, 1992). The short retention time might actually be an adaptation to eating fruit because large quantities of fruit must be processed to obtain an adequate protein intake. In contrast, when eating insects, robins (as well as other bird species) exhibit a higher digestive efficiency of approximately 70 percent (Levey and Karasov, 1989). Moreover, the energy content of insects tends to be higher than that of most fruits, particularly on a wet-weight basis (see Chapter 4). Thus, during the spring when robins are consuming insects, they should consume a smaller amount relative to their body weight than when eating fruits (Chapter 4 provides approaches that can be used to estimate insect ingestion rates for robins).

***Molt*. Postjuvenile and postbreeding (prebasic) molts occur from late July to October (Wheelwright, 1986; Sharp, 1990). During this molt, robins are consuming largely fruits and other plant materials, which contain limited proteins. This may contribute to larger fruit consumption rates at this time. During the prebreeding (prealternate) molt, robins are feeding primarily on insects and other invertebrates (letter**

from N.T. Wheelright, Department of Biology, Bowdoin College, Brunswick, ME, to Sue Norton, March 18, 1992).

***Migration*. Most robins nesting in the northern United States and Canada winter in the Gulf Coast States and the Carolinas (Speirs, 1953; Dorst, 1962, as cited in Henny, 1972). Wintering robins are most abundant between 30 and 35 degrees N latitude (Speirs, 1953). Robin flocks migrate during the day (Robbins et al., 1983); most northern robins leave their breeding grounds from September to November and return between February and April (Howell, 1942; Young, 1951; Fuller, 1977).**

***Breeding activities and social organization*. The onset of the breeding season is later at higher latitudes (approximately 3 days for each additional degree in the east) and altitudes, but mating and egg laying generally occur in April or May (James and Shugart, 1974; Knupp et al., 1977). Males arrive on the breeding grounds before females to establish territories; females pair with established males, usually for the duration of the breeding season (Young, 1951). The female primarily builds the nest out of mud, dried grass, weedy stems, and other materials, constructing it on horizontal limbs, tree-branch crotches, within shrubs, or on any one of a number of man-made structures with horizontal surfaces (Howell, 1942; Klimstra and Stieglitz, 1957). First clutches usually contain three or four eggs; later clutches tend to contain fewer eggs (Young, 1955). The female does all of the incubating, which continues for 10 to 14 days following the laying of the second egg (Klimstra and Stieglitz, 1957; Young, 1955). Both males and females feed the nestlings (Young, 1955). Following fledging, the brood often divides, with the male and female each feeding half of the fledglings for another 2 weeks (Weatherhead and McRae, 1990). Females may start another brood before the current one is independent, leaving the male to feed all of the fledglings (Young, 1955). After reaching independence, juveniles often form foraging flocks in areas of high food availability (Hirth et al., 1969).**

Early in the breeding season, robins often roost communally. Males can continue to use these roosts throughout the breeding season, whereas females stop once they begin incubating eggs (Howell, 1940; Pitts, 1984). As fall approaches and their diet turns more toward fruits, robins in many areas begin to roost communally again and may join other species, such as common grackles and European starlings, in large roosts (Morrison and Caccamise, 1990).

***Home range and resources*. During the breeding season, male robins establish breeding territories, which the female helps to defend against other robins. Nonetheless, the territories of different pairs often overlap where neither pair can establish dominance (Young, 1951). Most foraging during the breeding season is confined to the territory, but adults sometimes leave to forage in more productive areas that are shared with other individuals (Howell, 1942; Young, 1951; Pitts, 1984). In some prime nesting areas (e.g., dense coniferous forest), where robin densities are high, territories are small and the birds might often forage elsewhere (Howell, 1942). Adult robins often return to the same territory in succeeding years (Young, 1951). During the nonbreeding roosting period, robins are likely to return to the same foraging sites for many weeks and to join roosts within 1 to 3 km of these foraging areas (Morrison and Caccamise, 1990).**

***Population density*. Nesting population density varies with habitat quality. Densely forested areas that provide well-protected nest sites have been found to support high densities of nesting robins; however, the relatively small territories found in these areas might not be used as much for foraging as those containing open areas (Howell, 1942). In the nonbreeding season, robins often join single- or mixed-species roosts that can include tens of thousands of birds (Morrison and Caccamise, 1990). Wintering robins are most common in pine or oak pine communities of the southeastern and southcentral United States, and decrease in abundance in drier, less forested areas westward (Speirs, 1953).**

***Population dynamics*. Robins first attempt to breed the year after they hatch (Henny, 1972) and will raise multiple broods in a season (Howell, 1942). Predation is often a major source of mortality for both eggs and nestlings (Knupp et al., 1977; Klimstra and Stieglitz, 1957). Approximately half of the adult birds survive from year to year (Farner, 1949; Henny, 1972); the average longevity of a robin that survives to its first January is from 1.3 to 1.4 years (Farner, 1949).**

Similar species (from general references)

- **The wood thrush (*Hylocichla mustelina*), which is smaller than the robin (18 cm), co-occurs with the robin in some woodland habitats but is only present in the eastern United States. This species nests primarily in the interiors of mature forests and has been decreasing in abundance over the past decade as forested habitats in North America become increasingly fragmented (Robbins et al., 1989; Terborgh, 1989). This species is also primarily a summer resident, wintering in Florida and the neotropics.**

- **The hermit thrush (*Catharus guttatus*) is found in coniferous and mixed woodlands at northerly latitudes or high elevations and winters primarily in the southern half of the United States. This species is also significantly smaller (15 cm) than the robin.**

- **Swainson's thrush (*Catharus ustulatus*) is present in the western and northeastern United States during the summer months, wintering in the neotropics. It is also smaller than the robin (16 cm).**

- **The varied thrush (*Ixoreus naevius*) occurs in moist coniferous forests of the Pacific Northwest. This bird is similar in size (21 cm) to the robin.**

General references

Howell (1942); Young (1955); National Geographic Society (1987); Robbins et al. (1983); Sharp (1990).

American Robin (*Turdus migratorius*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Body Weight (g)	A B all seas.	77.3 ± 0.36 SE	63.5 - 103	Pennsylvania	Clench & Leberman, 1978	1
	A M nonbreed. A F nonbreed.	86.2 ± 6.1 SD 83.6 ± 6.4 SD		New York	Wheelwright, 1986	
	A M breeding A F breeding	77.4 80.6		New York	Wheelwright, 1986	
	nestlings: at hatching day 2 day 4 day 6 day 8 day 10 day 14	 5.5 12.6 24.3 39.4 50.9 55.2 55.0	 4.1 - 6.7 8.4 - 17.5 17.9 - 32.3 32.5 - 45.9 42.0 - 59.3 49.0 - 63.2 51.8 - 58.2	 New York/forest	 Howell, 1942	
Egg Weight (g)		6.26	4.6 - 8.4	New York	Howell, 1942	
Metabolic Rate (kcal/kg-day)	A B basal	259			estimated	2
	- B existence	344		Kansas	Hazelton et al., 1984 (estimate)	3
	A B free-living	713	(336 - 1,513)		estimated	4
Food Ingestion Rate (kcal/kg- day)	A B free-living	1,070 ± 220 SD	760 - 1,330	Kansas	Hazelton et al., 1984	5
Food Ingestion Rate (g/g-day)	B B free-living	0.89 ± 0.73 SD		California	Skorupa & Hothem, 1985	6
	- B free-living	1.52 ± 0.25 SD	1.22 - 1.96	Kansas	Hazelton et al., 1984	7
Water Ingestion Rate (g/g-day)	A B	0.14			estimated	8

American Robin (*Turdus migratorius*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location or subspecies	Reference	Note No.
Surface Area (cm^2)	A B	198			Walsberg & King, 1978	9
	A B	182			estimated	10

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
nestlings/fledglings:					south central New York/forest	Howell, 1942	
earthworms		15.0					
sowbugs		1.7					
spiders		2.3			(% wet weight; stomach contents)		
millipedes		3.1					
short-horned grass-hoppers		4.9			(age of robins ranged from 3 to 35 days after hatching; presence of grass is likely to be accidental - carried along with prey)		
beetles		11.6					
lepidopteran larvae		24.7					
ants		3.2					
unidentified animal		5.2					
grass (all parts)		19.5					
mulberries		3.2					
honeysuckle seeds		2.4					
unidentified plants		4.2					
adults:					eastern United States (% volume; stomach contents)	Wheelwright, 1986	11
fruit	7	68	92	83			
invertebrates	93	32	8	17			
adults:					central United States (% volume; stomach contents)	Wheelwright, 1986	11
fruit	8	41	76	73			
invertebrates	92	59	24	27			
adults:					western United States (% volume; stomach contents)	Wheelwright, 1986	11
fruit	17	29	63	70			
invertebrates	83	71	37	30			

American Robin (*Turdus migratorius*)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory Size (ha)	spring A B A B A B	 0.42 0.11 0.21	 0.12 - 0.84	 Tennessee/campus New York/dense conifers /unspecified forest	 Pitts, 1984 Howell, 1942	 12
Foraging Home Range (ha)	summer, adults feeding: nestlings fledglings	 0.15 ± 0.021 SE 0.81 ± 0.13 SE		 Ontario/deciduous forest	 Weatherhead & McRae, 1990	
Population Density (pairs/ha)	spring A B A B A B	 1.98 ± 0.48 SD 8.6 4.9	 1.39 - 2.54	 Tennessee/campus New York/dense conifers /unspecified forest	 Pitts, 1984 Howell, 1942	
Clutch Size		3.17 3.45 ± 0.59 SD	1 - 5 1 - 5	Illinois/suburban Wisconsin/park	Klimstra & Stieglitz, 1957 Young, 1955	
Clutches/Year		2	1 - 3	New York/forest	Howell, 1942	
Days Incubation		12.5 ± 0.14 SE	10 - 14	Wisconsin/park	Young, 1955	13
Age at Fledging (days)	B	13.4 ± 0.13 SE		Wisconsin/park	Young, 1955	
Number Fledge per Breeding Pair		5.6 3.9 1.5 ± 0.45 SE		Wisconsin/park New York/forest Ontario/deciduous forest	Young, 1955 Howell, 1942 Weatherhead & McRae, 1990	
Number Fledge per Successful Nest	five areas	2.9 2.5 ± 0.15 SD	2.4 - 3.4 (over 5 areas)	Wisconsin/park Maine/forest	Young, 1955 Knupp et al., 1977	

American Robin (*Turdus migratorius*)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Age at Sexual Maturity	B	1 year		NS	Henny, 1972	
Annual Mortality Rates (percent)	A B J B	51 ± 0.5 SE 78 - 82		North America	Henny, 1972	
Longevity (years)	after Jan. 1 of first year	1.3 - 1.4	up to 9	North America	Farner, 1949	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	early April late April early May	mid-April late May	late April mid-July early July	Illinois south central New York n Maine	Klimstra & Stieglitz, 1957 Howell, 1942 Knupp et al., 1977	
Hatching	early May early May mid-May mid-April early June			west: California, New Mexico east: VA, WV, DC, NY northeast: VT, NH, CT Kentucky Colorado	James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974	
Molt fall		July & August		North America	Wheelwright, 1986	
Migration fall	mid-Sept.	mid-October	early November early November	migrating through Minnesota leaving New York	Fuller, 1977 Howell, 1942	
spring	February mid-March		March mid-April	arriving New York arriving Wisconsin	Howell, 1942 Young, 1951	

1 As cited in Dunning (1984).
2 Estimated using equation 3-27 (Lasiewski and Dawson, 1967) and body weights from Clench and Leberman (1978).
3 Hazelton et al. (1984) estimate using Kendeigh's (1969) equations for a 55-g bird.
4 Estimated using equation 3-36 (Nagy, 1987) and body weights from Clench and Leberman (1978).

American Robin (*Turdus migratorius*)

5 Estimated kcal consumed in feeding trials. Diet consisted of paired offerings of fruit (to test preferences) over a 2-day period, 12 trials per pairing. Fruit included strawberries (2.29 kcal/g), cherries (4.34 kcal/g), green grapes (2.59 kcal/g), and purple grapes (5.85 kcal/g). Mean weight of the birds = 55 g.

6 Based on gizzard contents of robins caught foraging in vineyards; diet 85 percent (wet weight) grapes, 11.5 percent invertebrates, and 4.5 percent other plants. Mean weight of the birds = 82.3 g.

7 Based on same study described in note 5 and estimated weights of fruits consumed.

8 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Clench and Leberman (1978).

9 Beak surface area 3.1 cm^2; leg surface area 14.0 cm^2.

10 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Clench and Leberman (1978).

11 The U.S. Biological Survey and U.S. Fish and Wildlife Service records on which this study is based have several limitations: more birds were collected in agricultural and suburban than natural areas; seasons and time of day of collection were convenient to the collectors; quickly digested foods such as earthworms and other soft-bodied insects are underrepresented.

12 Birds nesting in high densities in dense coniferous forest probably foraged elsewhere more of the time than did birds with larger territories in less dense forests.

13 Also included data from Howell (1942) (Ithaca, New York) in calculations.

References (including Appendix)

Aldrich, J. W.; James, F. C. (1991) Ecogeographic variation in the American robin (*Turdus migratorius*). Auk 108: 230-249.

Armstrong, J. T. (1965) Breeding home range in the nighthawk and other birds: its evolutionary and ecological significance. Ecology 46: 619-629.

Baird, J. W. (1980) The selection and use of fruit by birds in an eastern forest. Wilson Bull. 92: 63-73.

Bovitz, P. (1990) Relationships of foraging substrate selection and roosting in American robins and European starlings [master's thesis]. New Brunswick, NJ: Rutgers University.

Brackbill, H. (1952) Three-brooded American robin. Bird-Banding 23: 29.

Butts, W. K. (1927) The feeding range of certain birds. Auk 44: 329-350.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Clench, M. H.; Leberman, R. C. (1978) Weights of 151 species of Pennsylvania birds analyzed by month, age, and sex. Bull. Carnegie Mus. Nat. Hist.

Dorst, J. (1962) The migration of birds. Boston: Houghton Mifflin Co.

Dunning, J. B., Jr. (1984) Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. Cave Creek, AZ: Eldon Publishing.

Farner, D. S. (1945) Age groups and longevity in the American robin. Wilson Bull. 57: 56-74.

Farner, D. S. (1949) Age groups and longevity in the American robin: comments, further discussion, and certain revisions. Wilson Bull. 61: 68-81.

Fuller, P. (1977) Fall robin migration. Loon 49: 239-240.

Gochfeld, M.; Burger, J. (1984) Age differences in foraging behavior of the American robin (*Turdus migratorius*). Behaviour 88: 227-239.

Hamilton, W. J., Jr. (1940) Summer food of the robin determined by fecal analyses. Wilson Bull. 52: 79-82.

Hamilton, W. J., Jr. (1943) Spring food of the robin in central New York. Auk 60: 273.

Hazelton, P. K., Robel, R. J.; Dayton, A. D. (1984) Preferences and influences of paired food items on energy intake of American robins (*Turdus migratorius*) and gray catbirds (*Dumetella carolinensis*). J. Wildl. Manage 48: 198-202.

Henny, C. J. (1972) An analysis of the population dynamics of selected avian species with special reference to changes during the modern pesticide era. Washington, DC: Bur. Sport. Fish. Wildl., Wildl. Res. Rep. 1.

Hirth, D. H.; Hester, A. E.; Greeley, F. (1969) Dispersal and flocking of marked young robins (*Turdus m. migratorius*) after fledging. Bird-Banding 40: 208-215.

Howell, J. C. (1940) Spring roosts of the robin. Wilson Bull. 52: 19-23.

Howell, J. C. (1942) Notes on the nesting habits of the American robin (*Turdus migratorius* L.). Am. Midl. Nat. 28: 529-603.

James, F. C.; Shugart, H. H. (1974) The phenology of the nesting season of the American robin (*Turdus migratorius*) in the United States. Condor 76: 159-168.

Jung, R. E. (1992) Individual variation in fruit choice by American robins *Turdus migratorius*. Auk 109: 98-111.

Karasov, W. H.; Levey, D. J. (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. Physiol. Zool. 63: 1248-1270.

Kendeigh, S. C. (1969) Tolerance of cold and Bergmann's rule. Auk 86: 13-25.

Klimstra, W. D.; Stieglitz, W. O. (1957) Notes on reproductive activities of robins in Iowa and Illinois. Wilson Bull. 69: 333-337.

Knupp, D. M.; Owen, R. B.; Dimond, J. B. (1977) Reproductive biology of American robins in northern Maine. Auk 94: 80-85.

Lasiewski, R. C.; Dawson, W. R. (1967). A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 12-23.

Levey, D. J.; Karasov, W. H. (1989) Digestive responses of temperate birds switched to fruit or insect diets. Auk 106: 675-686.

Levey, D. J.; Karasov, W. H. (1992) Digestive modulation in a seasonal frugivore: the American robin *Turdus migratorius*. Am. J. Physiol. 262: G711-G718.

Malmborg, P. K.; Willson, M. F. (1988) Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. Condor 90: 173-186.

Martin, A. C.; Zim, H. S.; Nelson, A. L. (1951) American wildlife and plants. New York, NY: McGraw-Hill Book Company, Inc.

Meeh, K. (1879) Oberflachenmessungen des mensclichen Korpers. Z. Biol. 15: 426-458.

Morrison, D. W.; Caccamise, D. F. (1990) Comparison of roost use by three species of communal roostmates. Condor 92: 405-412.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

National Geographic Society. (1987) Field guide to the birds of North America. Washington, DC: National Geographic Society.

Paszkowski, C. A. (1982) Vegetation, ground, and frugivorous foraging of the American robin *Turdus migratorius*. Auk 99: 701-709.

Pitts, T. D. (1984) Description of American robin territories in northwest Tennessee. Migrant 55: 1-6.

Robbins, C. S.; Bruun, B.; Zim, H. S. (1983) A guide to field identification: birds of North America. New York, NY: Golden Press.

Robbins, C. S.; Sauer, J. R.; Greenberg, R. S.; et al. (1989) Population declines in North American birds that migrate to the neotropics. Proc. Natl. Acad. Sci. USA 86: 7658-7662.

Rubner, M. (1883) Uber den Einfluss der Korpergrosse auf Stoff- und Kraftweschsel. Z. Biol. 19: 535-562.

Sharp, M. H. (1990) America's songbird--species profile: American robin (*Turdus migratorius*). Wild Bird 4: 22-27.

Skorupa, J. P.; Hothem, R. L. (1985) Consumption of commercially-grown grapes by American robins (*Turdus migratorius*): a field evaluation of laboratory estimates. J. Field Ornithol. 56: 369-378.

Speirs, J. M. (1953) Winter distribution of robins east of the Rocky Mountains. Wilson Bull. 65: 175-183.

Terborgh, J. (1989). Where have all the birds gone? Princeton, NJ: Princeton University Press.

Walsberg, G. E.; King, J. R. (1978) The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76: 185-189.

Weatherhead, P. J.; McRae, S. B. (1990) Brood care in American robins: implications for mixed reproductive strategies by females. Anim. Behav. 39: 1179-1188.

Wheelwright, N. T. (1986) The diet of American robins: an analysis of U.S. Biological Survey records. Auk 103: 710-725.

Wheelwright, N. T. (1988) Seasonal changes in food preferences of American robins in captivity. Auk 105: 374-378.

Young, H. (1951) Territorial behavior of the eastern robin. Proc. Linnean Soc. N.Y. 58-62: 1-37.

Young, H. (1955) Breeding behavior and nesting of the eastern robin. Am. Midl. Nat. 53: 329-352.

2.2. MAMMALS

Table 2-2 lists the mammalian species described in this section. For range maps, refer to the general references identified in the individual species profiles. The remainder of this section is organized by species in the order presented in Table 2-2. The availability of information in the published literature varies substantially among species, as is reflected in the profiles. Some of the selected species include two or more subspecies; these are indicated in the profiles when reported by the investigators. Body lengths of the mammals are reported for the length of the outstretched animal from the tip of the nose to the base of the tail. The tail measurements do not include the hairs at the tip, but only the tail vertebrae. Body weight is reported as fresh wet weight with pelage, unless otherwise noted.

Table 2-2. Mammals Included in the Handbook

Order Subfamily	Common name	Scientific name	Section
Soricidae	**short-tailed shrew**	***Blarina brevicauda***	**2.2.1**
Canidae	**red fox**	***Vulpes vulpes***	**2.2.2**
Procyonidae	**raccoon**	***Procyon lotor***	**2.2.3**
Mustelidae			
Mustelinae	**mink**	***Mustela vison***	**2.2.4**
Lutrinae	**river otter**	***Lutra canadensis***	**2.2.5**
Phocidae	**harbor seal**	***Phoca vitulina***	**2.2.6**
Cricetidae			
Sigmodontinae	**deer mouse**	***Peromyscus maniculatus***	**2.2.7**
Arvicolinae	**prairie vole**	***Microtus ochrogaster***	**2.2.8**
	meadow vole	***Microtus pennsylvanicus***	**2.2.9**
	muskrat	***Ondatra zibethicus***	**2.2.10**
Leporidae	**eastern cottontail**	***Sylvilagus floridanus***	**2.2.11**

2.2.1. Short-Tailed Shrew (shrews)

Order *Insectivora*, Family *Soricidae*. Shrews are small insectivorous mammals that inhabit most regions of the United States. They have high metabolic rates and can eat approximately their body weight in food each day. Most species are primarily vermivorous and insectivorous, but some also eat small birds and mammals.

Selected species

The northern short-tailed shrew (*Blarina brevicauda)* ranges throughout the north-central and northeastern United States and into southern Canada (George et al., 1986). It eats insects, worms, snails, and other invertebrates and also may eat mice, voles, frogs, and other vertebrates (Robinson and Brodie, 1982). Because they prey on other vertebrates, shrews can concentrate DDT (and presumably other bioaccumulative chemicals) to levels 10 times higher than either *Peromyscus* and *Clethrionomys* (Dimond and Sherburne, 1969). Shrews are an important component of the diet of many owls (Palmer and Fowler, 1975; Burt and Grossenheider, 1980) and are also prey for other raptors, fox, weasels, and other carnivorous mammals (Buckner, 1966).

***Body size*. Short-tailed shrews are 8 to 10 cm in length with a 1.9 to 3.0 cm tail (Burt and Grossenheider, 1980). The short-tailed shrew is the largest member of the genus, with some weighing over 22 g (George et al., 1986; see table). Some studies have found little or no sexual dimorphism in size (Choate, 1972), while other reports show that males are slightly larger than females (George et al., 1986; Guilday, 1957).**

***Metabolism*. Short-tailed shrews are active for about 16 percent of each 24-hour period (Martinsen, 1969), in periods of around 4.5 minutes at a time (Buckner, 1964). The shrew's metabolism is inversely proportional to the ambient temperature, within the range of 0 to 25°C (Randolph, 1973). Sleeping metabolism is half that associated with normal, exploring activity (Randolph, 1973). Randolph (1973) developed a regression equation for metabolism (cc O_2/g-hour) during (1) interrupted sleep:[e]**

(Winter) $Y = 4.754 - 0.0869\ (X - 16.4305)$
(Summer) $Y = 5.3448 - 0.1732\ (X - 16.2310)$

and (2) normal exploring activity:

(Winter) $Y = 6.5425 - 0.0516\ (X - 12.0600)$
(Summer) $Y = 7.949 - 0.2364\ (X - 16.9554)$ where X= ambient temperature in °C.

Randolph (1973) also developed a regression equation for overall metabolism (cal/animal-hour) for shrews spending equal amounts of time sleeping and exploring (cal/animal-hour) as a function of ambient temperature:

---

[e]Randolph's (1973) equations could be simplified to match that of Deavers and Hudson (1981; next page) in form; however, we report the equations as Randolph reported them.

(Winter) $Y = 583.83 - 7.53 (X - 13.68)$
(Summer) $Y = 544.86 - 20.37 (X - 16.33)$, where X= ambient temperature in °C.

Deavers and Hudson (1981) found a linear increase in standard (near basal) metabolism with decreasing temperature that is similar to that for interrupted sleep described above (Y = standard metabolism in cc O_2/g-hour):

$Y = 8.84 - 0.22 (X)$ where X= ambient temperature.

Deavers and Hudson (1981) found that within the thermoneutral zone, the standard metabolic rate of the short-tailed shrew is approximately 190 percent the metabolic rate predicted from body weight.

***Habitat*.** Short-tailed shrews inhabit a wide variety of habitats and are common in areas with abundant vegetative cover (Miller and Getz, 1977). Short-tailed shrews need cool, moist habitats because of their high metabolic and water-loss rates (Randolph, 1973).

***Food habits*.** The short-tailed shrew is primarily carnivorous. Stomach analyses indicate that insects, earthworms, slugs, and snails can make up most of the shrew's food, while plants, fungi, millipedes, centipedes, arachnids, and small mammals also are consumed (Hamilton, 1941; Whitaker and Ferraro, 1963). Small mammals are consumed more when invertebrates are less available (Allen, 1938; Platt and Blakeley, 1973, cited in George et al., 1986). Shrews are able to prey on small vertebrates because they produce a poison secretion in their salivary glands that is transmitted during biting (Pearson, 1942, cited in Eadie, 1952). The short-tailed shrew stores food, especially in the autumn and winter (Hamilton, 1930; Martin, 1984). Robinson and Brodie (1982) found that short-tailed shrews cached most (86.6 percent) of the prey captured; only 9.4 percent was consumed immediately. Short-tailed shrews consume approximately 40 percent more food in winter than in summer (Randolph, 1973). The shrew must consume water to compensate for its high evaporative water loss, despite the fact that it obtains water from both food and metabolic oxidation (Chew, 1951). Deavers and Hudson (1981) indicated that the short-tailed shrew's evaporative water loss increases with increasing ambient temperature even within its thermoneutral zone. Short-tailed shrews' digestive efficiency is about 90 percent (Randolph, 1973).

***Temperature regulation and molt*.** The short-tailed shrew does not undergo torpor but uses nonshivering thermogenesis (NST) to compensate for heat loss during cold stress in winter (Zegers and Merritt, 1987). The short-tailed shrew exhibits three molts. Two are seasonal molts, the first in October/November replaces summer with winter pelage and occurs in first- and second-year shrews. The spring molt can occur any time from February to October. The third molt occurs in postjuveniles that have reached adult size (Findley and Jones, 1956).

***Breeding activities and social organization*.** The short-tailed shrew probably breeds all year, including limited breeding in winter even in the northern portions of its range (Blus, 1971). In Illinois, males were found to be most active from January to July, females from March to September (Getz, 1989). There are two peak breeding periods, in

the spring and in late summer or early fall (Blair, 1940). The home ranges of short-tailed shrews in summer overlap both within and between sexes (Blair, 1940), although females with young do exhibit some territoriality (Platt, 1976). Nomadic shrews are either young of the year or adults moving to areas with more abundant prey (Platt, 1976).

***Home range and resources*. Short-tailed shrews inhabit round, underground nests and maintain underground runaways, usually in the top 10 cm of soil, but sometimes as deep as 50 cm (Hamilton, 1931; and Jameson, 1943, cited in George et al., 1986). Winter, nonbreeding home ranges can vary from 0.03 to 0.07 ha at high prey densities to 1 to 2.2 ha during low prey densities with a minimum of territory overlap. In the summer, ranges of opposite sex animals overlap, but same sex individuals do not; females with young exclude all others from their area (Platt, 1976).**

***Population density*. Population densities vary by habitat and season (Getz, 1989; Jackson, 1961; Platt, 1968). In east-central Illinois, population density was higher in bluegrass than in tallgrass or alfalfa (Getz, 1989). In all three of these habitats, the short-tailed shrew exhibited annual abundance cycles, with peak densities ranging from 2.5 to 45 shrews per hectare, depending on the habitat (Getz, 1989). The peaks occurred from July to October (12.9/ha average for all three habitats), apparently just following peak precipitation levels (Getz, 1989).**

***Population dynamics*. Winter mortality up to 90 percent has been reported for the short-tailed shrew (Barbehenn, 1958; Gottschang, 1965; Jackson, 1961, cited in George et al., 1986); however, Buckner (1966) suggests that mortality rates in winter may be closer to 70 percent, which is similar to the average monthly mortality rate he found for subadult animals. Several litters, averaging four to five pups, are born each year (George et al., 1986).**

Similar species (from general references)

- **The masked shrew (*Sorex cinereus*) (length 5.1 to 6.4 cm; weight 3 to 6 g) is smaller than the short-tailed shrew and is the most common shrew in moist forests, open country, and brush of the northern United States and throughout Canada and Alaska. It feeds primarily on insects.**

- **Merriam's shrew (*Sorex merriami*) (5.7 to 6.4 cm) is found in arid areas and sagebrush or bunchgrass of the western United States and is smaller than the short-tailed shrew.**

- **The smokey shrew (*Sorex fumeus*) (6.4 to 7.6 cm; 6 to 9 g), smaller than the short-tailed, prefers birch and hemlock forests with a thick leaf mold on the ground to burrow in. It uses burrows made by small mammals or nests in stumps, logs, and among rocks. Range is limited to the northeast United States and east of the Great Lakes in Canada.**

- **The southeastern shrew (*Sorex longirostris*) (5.1 to 6.4 cm; 3 to 6 g) prefers moist areas. Found mostly in open fields and woodlots, its range is limited**

to the southeastern United States. It nests in dry grass or leaves in a shallow depression.

- **The long-tailed shrew (*Sorex dispar*) (7.0 cm; 5 to 6 g) inhabits cool, moist, rocky areas in deciduous or deciduous-coniferous forests of the northeast, extending south to the North Carolina and Tennessee border.**

- **The vagrant shrew (*Sorex vagrans*) (5.9 to 7.3 cm; 7 ± g) inhabits marshy wetlands and forest streams. Its range is confined to the western United States, excluding most of California and Nevada. In addition to insects, it also eats plant material.**

- **The Pacific shrew (*Sorex pacificus*) (8.9 cm) is slightly larger than the short-tailed shrew. It is limited to redwood and spruce forests, marshes, and swamps of the northern California and southern Oregon coasts.**

- **The dwarf shrew (*Sorex nanus*) (6.4 cm) is rare throughout its limited range in the western United States.**

- **The least shrew (*Cryptotis parva*) (5.6 to 6.4 cm; 4 to 7 g) is easily distinguished from other shrews by its cinnamon color. It inhabits grassland and marsh; its range is similar to the short-tailed shrew but does not extend as far north.**

- **The desert shrew (*Notiosorex crawfordi*) (Gray shrew) (5.1 to 6.6 cm) is rarely seen and is found only in the arid conditions, chaparral slopes, alluvial fans, and around low desert shrubs of the extreme southwest. It nests beneath plants, boards, or debris.**

General references

Burt and Grossenheider (1980); George et al. (1986).

Short-Tailed Shrew (*Blarina brevicauda*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI)	Location	Reference	Note No.
Body Weight (g)	A B	15.0 ± 0.78 SD		New Hampshire	Schlesinger & Potter, 1974	
	M summer F summer M fall M fall	19.21 ± 0.42 SD 17.40 ± 0.48 SD 16.87 ± 0.21 SD 15.58 ± 0.23 SD	17.0 - 22.0 14.0 - 21.0 13.0 - 22.0 12.5 - 22.5	w Pennsylvania	Guilday, 1957	
	neonate		0.67 - 1.29	Maryland/lab	Blus, 1971	
Metabolic Rate (lO_2/kg-day)	basal average daily	82 125	80 - 84 106 - 150	Pennsylvania/lab	Pearson, 1947	1
	average daily	127 ± 15.3 SD	94 - 218	NS/lab	Morrison, 1948	2
	+ 20°C - 20°C	126.5 207.1		Ontario, CAN/lab	Randolph, 1973	
Metabolic Rate (kcal/kg-day)	basal average daily	390 600		Pennsylvania/lab	Pearson, 1947	3
	average daily	680		Wisconsin/lab	Morrison et al., 1957	4
Food Ingestion Rate	A B: 22 - 23°C	7.95 ±0.17 g/d SD 0.49 g/g-day		Ohio/lab	Barrett & Stuek, 1976	5
	A B: 25°C	0.62 g/g-day		Wisconsin/lab	Morrison et al., 1957	6
Water Ingestion Rate (g/g-day)	A B	0.223		Illinois/lab	Chew, 1951	
Inhalation Rate (m^3/day)	A B	0.026			estimated	7
Surface Area (cm^2)	A B	54		Pennsylvania/lab	Pearson, 1947	8
	A B	84			estimated	9

Short-Tailed Shrew (*Blarina brevicauda*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
earthworms		31.4			New York/NS (% volume; stomach contents) (June through October collections combined)	Whitaker & Ferraro, 1963	
slugs & snails		27.1					
misc. animals		8.1					
Endegon (fungi)		7.7					
beetles		5.9					
vegetation		5.4					
lepidopteran larvae		4.3					
chilopoda		1.8					
other		8.6					
insects		77.6			eastern United States (primarily New York)/NS (% frequency of occurrence; stomach contents) (all seasons combined)	Hamilton, 1941	
annelids		41.8					
vegetable matter		17.1					
centipedes		7.4					
arachnids		6.1					
snails		5.4					
small mammals		5.2					
crustacea		3.7					
undetermined		2.4					

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A F summer A M summer		< 0.1 - 0.36 < 0.1 - 1.8	s Michigan/bluegrass	Blair, 1940	
	B B all	0.39 ± 0.036 SD		s Manitoba/tamarack bog	Buckner, 1966	
	B B winter (a) B B winter (b)		0.03 - 0.07 0.10 - 0.22	c New York/old field	Platt, 1976	10

Short-Tailed Shrew (*Blarina brevicauda*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (N/ha)	winter spring summer fall	2.3 5.9 11.4 10.0		ec Illinois/alfalfa	Getz, 1989	
			1.6 - 121	Wisconsin/beech-maple	Jackson, 1961; Williams, 1936	11
	B B		0.06 - 0.16	Manitoba, Canada/ tamarack bog	Buckner, 1966	
Litter Size		5.4	2 - 8	Indiana/NS	French, 1984	
		4.7 ± 0.2 SE	1 - 8	Maryland/lab	Blus, 1971	
Litters /Year		several		NS/NS	George et al., 1986	
Days Gestation		21 - 22		Maryland/lab	Blus, 1971	12
Age at Weaning (days)		25 - 30		Maryland/lab	Blus, 1971	
Age at Sexual Maturity	M		$\geq$ 65 days	Maryland/lab	Blus, 1971	
	M		$\geq$ 83 days	NS/NS	Pearson, 1944	11
	F	< 1 year		Indiana/NS	French, 1984	
Annual Mortality	B B	93 %		MD, PA, NY, MA/NS	Pearson, 1945	
Longevity	M F	4.6 months 4.4 months		Maryland/lab	Blus, 1971	13
	B		$\leq$ 20 months	c New York/woods, field	Dapson, 1968	

Short-Tailed Shrew (*Blarina brevicauda*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	late February	April - May	mid-September	Indiana	French, 1984	
Parturition		May - June		c New York	Dapson, 1968	
Molt fall	October		November	NS	Findley & Jones, 1956	11
spring	February		July	NS	Findley & Jones, 1956	11

1 Ambient temperatures 25 to 30°C; mean weight of shrews = 21.2 g.
2 Ambient temperatures 15 to 25°C; mean weight of shrews = 21 g.
3 Calculated from oxygen consumption rate; mean weight of shrews = 21.2 g. Basal metabolism is 186 percent higher than predicted from equations 3-42 or 3-43, in agreement with the finding of Deavers and Hudson (1981). Average daily metabolism was estimated over 24-hour period at 25 to 30°C and is 146 percent higher than the free-living metabolic rate predicted on the basis of equation 3-47 (Nagy, 1987).
4 Calculated from average food consumption rate (liver; 1.22 kcal/g wet weight) at 25°C. This value is 167 percent higher than the free-living metabolic rate predicted on the basis of equation 3-47 (Nagy, 1987).
5 Diet of mealworms estimated to provide 2.33 kcal/g live weight. Assimilation efficiency for shrews consuming mealworms = 89.5 ± 1.9 SD.
6 Diet of beef liver; mean weight of shrews = 21 g.
7 Estimated using equation 3-20 (Stahl, 1967) and adult male summer body weights from Guilday (1957).
8 Estimate for 21.2-g shrew.
9 Estimated using equation 3-22 (Stahl, 1967) and adult male summer body weights from Guilday (1957).
10 (a) At high prey density; (b) at low prey density.
11 Cited in George et al. (1986).
12 From pairing to parturition.
13 Mean longevity of animals that survived to weaning.

References (including Appendix)

Allen, D. L. (1938) Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. Ecol. Monogr. 8: 347-436.

Barbehenn, K. R. (1958) Spatial and population relationships between *Microtus* and *Blarina*. Ecology 39: 293-304.

Barrett, G. W.; Stueck, K. L. (1976) Caloric ingestion rate and assimilation efficiency of the short-tailed shrew, *Blarina brevicauda*. Ohio J. Sci. 76: 25-26.

Blair, W. F. (1940) Notes on home ranges and populations of the short-tailed shrew. Ecology 21: 284-288.

Blair, W. F. (1941) Some data on the home ranges and general life history of short-tailed shrews, red-backed voles and woodland jumping mice in northern Michigan. Am. Midl. Nat. 25: 681-685.

Blus, L. J. (1971) Reproduction and survival of short-tailed shrews (*Blarina brevicauda*) in captivity. Lab. Anim. Sci. 21: 884-891.

Buckner, C. H. (1964) Metabolism, food capacity, and feeding behavior in four species of shrews. Can. J. Zool. 42: 259-279.

Buckner, C. H. (1966) Populations and ecological relationships of shrews in tamarack bogs of southeastern Manitoba. J. Mammal. 47: 181-194.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Chew, R. M. (1951) The water exchanges of some small mammals. Ecol. Monogr. 21: 215-225.

Choate, J. R. (1972) Variation within and among populations of short-tailed shrews, *Blarina brevicauda*. J. Mammal. 53: 116-128.

Dapson, R. W. (1968) Reproduction and age structure in a population of short-tailed shrews, *Blarina brevicauda*. J. Mammal. 49: 205-214.

Deavers, D. R.; Hudson, J. W. (1981) Temperature regulation in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and a shrew (*Blarina brevicauda*) inhabiting the same environment. Physiol. Zool. 54: 94-108.

Dimond, J. B.; Sherburne, J. A. (1969) Persistence of DDT in wild populations of small mammals. Nature 221: 486-487.

Eadie, R. W. (1952) Shrew predation and vole populations on a localized area. J. Mammal. 33: 185-189.

Findley, J. S.; Jones, J. K., Jr. (1956) Molt of the short-tailed shrew, *Blarina brevicauda*. Am. Midl. Nat. 56: 246-249.

French, T. W. (1984) Reproduction and age structure of three Indiana shrews. Proc. Indiana Acad. Sci. 94: 641-644.

George, S. B.; Choate, J. R.; Genoways, H. H. (1986) *Blarina brevicauda*. American Society of Mammalogists; Mammalian Species 261.

Getz, L. L. (1989) A 14-year study of *Blarina brevicauda* populations in east-central Illinois. J. Mammal. 70: 58-66.

Gottschang, J. L. (1965) Winter populations of small mammals in old fields of southwestern Ohio. J. Mammal. 46: 44-52.

Guilday, J. E. (1957) Individual and geographic variation in *Blarina brevicauda* from Pennsylvania. Ann. Carnegie Mus. 35: 41-68.

Hamilton, W. J., Jr. (1929) Breeding habits of the short-tailed shrew, *Blarina brevicauda*. J. Mammal. 10: 125-134.

Hamilton, W. J., Jr. (1930) The food of the Soricidae. J. Mammal. 11: 26-39.

Hamilton, W. J., Jr. (1931) Habits of the short-tailed shrew, *Blarina brevicauda* (Say). Ohio J. Sci. 31: 97-106.

Hamilton, W. J., Jr. (1941) The foods of small forest mammals in eastern United States. J. Mammal. 22: 250-263.

Jackson, H. H. T. (1961) Mammals of Wisconsin. Madison, WI: University of Wisconsin Press.

Jameson, E. W., Jr. (1943) Notes on the habits and siphanapterous parasites of the mammals of Welland County, Ontario. J. Mammal. 24: 194-197.

Lomolino, M. V. (1984) Immigrant selection, predation, and the distribution of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. Am. Nat. 123: 468-483.

Martin, I. G. (1984) Factors affecting food hoarding in the short-tailed shrew *Blarina brevicauda*. Mammalia 48: 65-71.

Martinsen, D. L. (1969) Energetics and activity patterns of short-tailed shrews (*Blarina*) on restricted diets. Ecology 50: 505-510.

Miller, H.; Getz, L. L. (1977) Factors influencing local distribution and species diversity of forest small mammals in new England. Can. J. Zool. 55: 806-814.

Morrison, P. R. (1948) Oxygen consumption in several small wild mammals. J. Cell. Comp. Physiol. 31: 69-96.

Morrison, P. R.; Pierce, M.; Ryser, F. A. (1957) Food consumption and body weight in the masked and short-tailed shrews (genus *Blarina*) in Kansas, Iowa, and Missouri. Ann. Carnegie Mus. 51: 157-180.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Mono. 57: 111-128.

Neal, C. M.; Lustick, S. I. (1973) Energetics and evaporative water loss in the short-tailed shrew *Blarina brevicauda*. Physiol. Zool. 46: 180-185.

Palmer, E. L.; Fowler, H. S. (1975) Fieldbook of natural history. New York, NY: McGraw-Hill Book Co.

Pearson, O. P. (1942) The cause and nature of a poisonous action produced by the bite of a shrew (*Blarina brevicauda*). J. Mammal. 23: 159-166.

Pearson, O. P. (1944) Reproduction in the shrew (*Blarina brevicauda* Say). Am. J. Anat. 75: 39-93.

Pearson, O. P. (1945) Longevity of the short-tailed shrew. Am. Midl. Nat. 34: 531-546.

Pearson, O. P. (1947) The rate of metabolism of some small mammals. Ecology 29: 127-145.

Platt, A. P. (1968) Differential trap mortality as a measure of stress during times of population increase and decrease. J. Mammal. 49: 331-335.

Platt, W. J. (1974) Metabolic rates of short-tailed shrews. Physiol. Zool. 47: 75-90.

Platt, W. J. (1976) The social organization and territoriality of short-tailed shrew (*Blarina brevicauda*) populations in old-field habitats. Anim. Behav. 24: 305-318.

Platt, W. J.; Blakeley, N. R. (1973) Short-term effects of shrew predation upon invertebrate prey sets in prairie ecosystems. Proc. Iowa Acad. Sci. 80: 60-66.

Randolph, J. C. (1973) Ecological energetics of a homeothermic predator, the short-tailed shrew. Ecology 54: 1166-1187.

Richardson, J. H. (1973) Locomotory and feeding activity of the shrews, *Blarina brevicauda* and *Suncus murinus*. Am. Midl. Nat. 90: 224-227.

Robinson, D. E.; Brodie, E. D. (1982) Food hoarding behavior in the short-tailed shrew *Blarina brevicauda*. Am. Midl. Nat. 108: 369-375.

Schlesinger, W. H.; Potter, G. L. (1974) Lead, copper, and cadmium concentrations in small mammals in the Hubbard Brook Experimental Forest. Oikos 25:148-152.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Whitaker, J. O., Jr.; Ferraro, M. G. (1963) Summer food of 220 short-tailed shrews from Ithaca, New York. J. Mammal. 44: 419.

Williams, A. B. (1936) The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6: 317-408.

Zegers, D. A.; Merritt, J. F. (1987) Adaptations of *Peromyscus* for winter survival in an Appalachian montane forest. J. Mammal. 69: 516-523.

2.2.2. Red Fox (foxes and coyotes)

<u>Order *Carnivora*, Family *Canidae*</u>. Unlike the more social wolves, foxes and coyotes tend to hunt alone, although coyotes may hunt larger prey in pairs. Foxes and coyotes are primarily carnivorous, preying predominantly on small mammals, but they also may eat insects, fruits, berries, seeds, and nuts. Foxes are found throughout most of the United States and Canada, including the arctic, as are coyotes with the exception of the southeastern United States. Foxes and coyotes are active primarily at night.

Selected species

Red foxes (*Vulpes vulpes*) are present throughout the United States and Canada except in the southeast, extreme southwest, and parts of the central states. Red fox prey extensively on mice and voles but also feed on other small mammals, insects, hares, game birds, poultry, and occasionally seeds, berries, and fruits (Palmer and Fowler, 1975). Twelve subspecies are recognized in North America (Ables, 1974).

Body size. **The dog-sized red fox has a body about 56 to 63 cm in length, with a 35 to 41 cm tail (Burt and Grossenheider, 1980). They weigh from 3 to 7 kg, with the males usually outweighing the females by about 1 kg (Voigt, 1987; see table).**

Habitat. **As the most widely distributed carnivore in the world, the red fox can live in habitats ranging from arctic areas to temperate deserts (Voigt, 1987). Red foxes utilize many types of habitat--cropland, rolling farmland, brush, pastures, hardwood stands, and coniferous forests (MacGregor, 1942; Eadie, 1943; Cook and Hamilton, 1944; Ables, 1974). They prefer areas with broken and diverse upland habitats such as occur in most agricultural areas (Ables, 1974; Samuel and Nelson, 1982; Voigt, 1987). They are rare or absent from continuous stands of pine forests in the southeast, moist conifer forests along the Pacific coast, and semiarid grasslands and deserts (Ables, 1974).**

Food habits**.** **The red fox feeds on both animal and plant material, mostly small mammals, birds, insects, and fruit (Korschgen, 1959; Samuel and Nelson, 1982). Meadow voles are a major food in most areas of North America; other common prey include mice and rabbits (Korschgen, 1959; Voigt, 1987). Game birds (e.g., ring-necked pheasant and ruffed grouse) and waterfowl are seasonally important prey in some areas (Pils and Martin, 1978; Sargeant, 1972; Voigt and Broadfoot, 1983). Plant material is most common in red fox diets in summer and fall when fruits, berries, and nuts become available (Johnson, 1970; Major and Sherburne, 1987). Red foxes often cache food in a hole for future use (Samuel and Nelson, 1982). They also are noted scavengers on carcasses or other refuse (Voigt, 1987). Most activity is nocturnal and at twilight (Nowak and Paradiso, 1983).**

Temperature regulation and molt**.** **In winter, foxes do not undergo hibernation or torpor; instead, they are active year-round. They undergo one molt per year, which usually begins in April and is finished by June. The winter coat is regrown by October or November in northern latitudes (Voigt, 1987).**

***Breeding activities and social organization*.** **Breeding occurs earlier in the south than in the red fox's northern ranges (Samuel and Nelson, 1982) (see table). A mated pair maintains a territory throughout the year, with the male contributing more to its defense than the female (Preston, 1975). Pups are born and reared in an underground den, and the male assists the female in rearing young, bringing food to the den for the pups (Samuel and Nelson, 1982). Pups first emerge from the den when 4 to 5 weeks old (Samuel and Nelson, 1982). Once considered solitary, red foxes now are reported to exhibit more complex social habits (MacDonald and Voigt, 1985). A fox family, the basic social unit, generally consists of a mated pair or one male and several related females (MacDonald, 1980; Voigt, 1987). The additional females are usually nonbreeders that often help the breeding female (Voigt, 1987).**

***Home range and resources*.** **The home ranges of individuals from the same family overlap considerably, constituting a family territory (Sargeant, 1972; Voigt and MacDonald, 1984). Territories of neighboring red fox families are largely nonoverlapping and contiguous, usually resulting in all parts of a landscape being occupied by foxes. Territory sizes range from less than 50 to over 3,000 ha (see table). Territories in urban areas tend to be smaller than those in rural areas (Ables, 1969). Adults visit most parts of their territory on a regular basis; however, they tend to concentrate their activities near to their dens, preferred hunting areas, abundant food supplies, and resting areas (Ables, 1974; Keenan, 1981). Territory boundaries often conform to physical landscape features such as well-traveled roads and streams (Ables, 1974). Territory defense is primarily by nonaggressive mechanisms involving urine scent-marking and avoidance behaviors. Scent marking occurs throughout the territory; there is little patrolling of territory boundaries. Each fox or family usually has a main underground den and one or more other burrows within the home range (Nowak and Paradiso, 1983). Most dens are abandoned burrows of other species (e.g., woodchucks, badgers) (Samuel and Nelson, 1982). Tunnels are up to 10 m in length and lead to a chamber 1 to 3 m below the surface (Nowak and Paradiso, 1983). Pup-rearing dens are the focal point of fox activity during spring and early summer. Foxes have some rest sites and usually forage away from the den (Voigt, 1987).**

Population density. **One red fox family per 100 to 1,000 ha is typical (Voigt, 1987; see table). Red foxes have larger home ranges where population densities are low and in poorer habitats (Voigt, 1987). Most young foxes, especially males, disperse before the age of 1 (Voigt, 1987), usually during September to March, with peaks in dispersal in October and November (Phillips et al., 1972; Storm et al., 1976).**

***Population dynamics*.** **Foxes usually produce pups their first year, except in extremely high density areas and in some years in northern portions of their range where they may delay breeding until the next season (Allen, 1984; Harris, 1979; Storm et al., 1976; Voigt and MacDonald, 1984). Litter size generally averages four to six pups (see table). The pups leave the den about 1 month after birth, and they are weaned by about 8 to 10 weeks of age (Ables, 1974). Red foxes incur high mortality rates as a result of shooting, trapping, disease, and accidents (e.g., roadkills) (Storm et al., 1976). Two factors that tend to limit red fox abundance are competition with other canids, especially coyotes, and seasonal limits on food availability (Voigt, 1987). Fecundity is higher in areas of high mortality and low population densities (Voigt, 1987).**

Similar species (from general references)

- **The arctic fox (*Alopex lagopus*) is smaller than the red fox (body length approximately 51 cm; weight 3.2 to 6.7 kg) and is restricted in its distribution to the arctic, found in the United States only in Alaska. This species primarily scavenges for food but also eats lemmings, hares, birds, and eggs as well as berries in season.**

- **The swift fox (*Vulpes velox*) is smaller than the red fox (body length 38 to 51 cm; weight 1.8 to 2.7 kg) and inhabits the deserts and plains of the southwest and central United States. It dens in ground burrows and feeds on small mammals and insects.**

- **The kit fox (*Vulpes macrotis*) is similar in size to the swift fox and is considered by some to be the same species, although it has noticeably larger ears. It inhabits the southwestern United States and prefers open, level, sandy areas and low desert vegetation. It feeds on small mammals and insects.**

- **The gray fox (*Urocyon cinereoargenteus*) is similar in size (body length 53 to 74 cm; weight 3.2 to 5.8 kg) to the red fox and ranges over most of the United States except the northwest and northern prairies, inhabiting chaparral, open forests, and rimrock regions. Secretive and nocturnal, gray foxes will climb trees to evade enemies. They feed primarily on small mammals but also eat insects, fruits, acorns, birds, and eggs.**

- **The coyote (*Canis latrans*) is much larger (body length 81 to 94 cm; weight 9 to 22 kg) than the red fox and is found throughout most of the United States (except possibly eastern), western Canada, and Alaska. It inhabits prairies, open woodlands, brushy and boulder-strewn areas, and dens in the ground. Coyotes share some feeding habits with the red fox but also scavenge and hunt larger prey in pairs.**

General references

Ables (1974); Burt and Grossenheider (1980); Palmer and Fowler (1975); Voigt (1987).

Red Fox (*Vulpes vulpes*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (kg)	A M spring A F spring	5.25 ± 0.18 SE 4.13 ± 0.11 SE	4.54 - 7.04 3.27 - 4.72	Illinois	Storm et al., 1976	
	A M fall A F fall	4.82 ± 0.081 SE 3.94 ± 0.079 SE	4.13 - 5.68 2.95 - 4.59	Iowa	Storm et al., 1976	
	neonate B at weaning B	0.102 ± 0.12 SD 0.70	0.071 - 0.109	Wisconsin North Dakota	Storm & Ables, 1966 Sargeant, 1978	
Pup Growth Rate (g/day)	birth to weaning	15.9		North Dakota/lab	Sargeant, 1978	
Metabolic Rate (kcal/kg-day)	J summer	193 ± 56 SD		Ohio/lab	Vogtsberger & Barrett, 1973	
	A M basal A F basal	47.9 51.1			estimated	1
	A M free-living A F free-living	161 168	(68 - 383) (71 - 400)		estimated	2
Food Ingestion Rate (g/g-day)	J 5-8 wks J 9-12 wks J 13-24 wks	0.16 0.12 0.11		North Dakota/lab	Sargeant, 1978	
	A before whelp F after whelp	0.075 0.14		North Dakota/captive	Sargeant, 1978	3
	A nonbreeding	0.069		North Dakota/captive	Sargeant, 1978	
Water Ingestion Rate (g/g-day)	A M A F	0.084 0.086			estimated	4
Inhalation Rate (m^3/day)	A M A F	2.0 1.7			estimated	5

Red Fox (*Vulpes vulpes*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Surface Area (cm^2)	A M A F	3,220 2,760			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
rabbits small mammals pheasant other birds misc. not accounted for				44.4 33.0 8.4 11.2 2.0 1.0	Nebraska/statewide (% wet volume; stomach contents)	Powell & Case, 1982	
mammals birds arthropods plants unspecified/other	92.2 2.4 0.2 4.6 0.6	37.1 43.2 11.6 6.3 1.8	61.7 0.2 4.2 31.1 2.8	65.0 8.6 <0.1 26.1 0.3	Illinois/farm and woods (% wet weight; stomach contents)	Knable, 1974	
rabbits mice/rats other mammals poultry carrion livestock birds invertebrates plant foods	24.8 24.2 4.0 21.0 12.9 9.8 0.6 trace 2.7	10.7 6.2 1.4 45.0 13.0 0.3 1.2 15.3 6.9	36.5 21.3 8.1 16.3 6.5 2.0 1.1 1.6 6.6	38.7 22.5 8.2 11.6 7.4 5.4 3.8 trace 2.1	Missouri (% wet volume; stomach contents)	Korschgen, 1959	
mammals birds arthropods plants unspecified/other				81.4 4.8 2.8 7.0 4.0	Maryland/Appalachian Province (fall & winter) (% wet weight; stomach contents)	Hockman & Chapman, 1983	

Red Fox (*Vulpes vulpes*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory size (ha)	A B summer A M summer A F summer	1,611 1,967 1,137	277 - 3,420 514 - 3,420 277 - 1,870	nw British Columbia/ alpine and subalpine	Jones & Theberge, 1982	
	A F spring	699 ± 137 SD	596 - 855	ec Minnesota/woods, fields, swamp	Sargeant, 1972	
	A M all year A F all year	717 96	 57 - 170	Wisconsin/diverse	Ables, 1969	
Population Density (N/ha)	B B spring	0.001		Canada/northern boreal forests/arctic tundra	Voigt, 1987	
	B B spring	0.01		s Ontario, Canada/southern habitats	Voigt, 1987	
	B B		0.046 - 0.077	"good fox range" in North America	Ables, 1974	
Litter Size		5.5		s Wisconsin/farm, marsh, pasture	Pils & Martin, 1978	7
		6.8	2 - 9	Illinois/farm and woods	Storm et al., 1976	8
		6.7	3 - 12	Iowa/farm and woods	Storm et al., 1976	7
		4.2		upper Michigan/NS	Switzenberg, 1950	8
		4.1		North Dakota/prairie potholes	Allen, 1984	7
Litters/Year		1		NS/NS	Samuel & Nelson, 1982	
Days Gestation		51 - 54		New York/NS	Sheldon, 1949	9
Age at Weaning		8 - 10 weeks		NS/NS	Ables, 1974	
Age at Sexual Maturity	F	10 months		Illinois, Iowa/farm woods	Storm et al., 1976	

Red Fox (*Vulpes vulpes*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Annual Mortality Rates (percent)	B B	79.4		s Wisconsin/various	Pils & Martin, 1978	
	J M J F A F A B	83 81 74 77		Illinois/Iowa/ farms and woods	Storm et al., 1976	
Longevity		< 1.5 yrs	up to 6 yrs	NS/NS	Storm et al., 1976	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early Dec.	late January	late February	Iowa	Storm et al., 1976	
	late December	Jan. - Feb.	March	New York	Layne & McKeon, 1956; Sheldon, 1949	9
	late January		early February	southern Ontario, Canada	Voigt, 1987	
	February		March	northern Ontario, Canada	Voigt, 1987	
Parturition		March		southern CAN	Voigt, 1987	
		late March, April		e North Dakota	Sargeant, 1972	
Molt	April		June	NS/NS	Voigt, 1987	
Disperal	late September		March	Illinois, Iowa	Storm et al., 1976	

1 Estimated using extrapolation equation 3-45 (Boddington, 1978) and body weights from Storm et al. (1976) (Illinois).
2 Estimated using extrapolation equation 3-47 (Nagy, 1987) and body weights from Storm et al. (1976) (Illinois).
3 Food consumption of an adult pair for 11 days prior to whelping (i.e., parturition) and of the adult female for the first 4 weeks after whelping.
4 Estimated using extrapolation equation 3-17 (Calder and Braun, 1983) and body weights from Storm et al. (1976) (Illinois).
5 Estimated using extrapolation equation 3-20 (Stahl, 1967) and body weights from Storm et al. (1976) (Illinois).
6 Estimated using extrapolation equation 3-22 (Stahl, 1967) and body weights from Storm et al. (1976) (Illinois).
7 Litter size determined from embryo count. Using placental scars generally overestimates litter size, and counting live pups often underestimates litter size (Allen, 1983; Lindstrom, 1981).
8 Method of determining litter size not specified.
9 Cited in Samuel and Nelson (1982).

References (including Appendix)

Ables, E. D. (1969) Home range studies of red foxes (*Vulpes vulpes*). J. Mammal. 50: 108-120.

Ables, E. D. (1974) Ecology of the red fox in North America. In: Fox, M. W., ed. The wild canids. New York, NY: Van Nostrand Reinhold; pp. 148-163.

Allen, S. H. (1983) Comparison of red fox litter sizes determined from counts of embryos and placental scars. J. Wildl. Manage. 47: 860-863.

Allen, S. H. (1984) Some aspects of reproductive performance in the red fox in North Dakota. J. Mammal. 65: 246-255.

Allen, S. H.; Gulke, J. (1981) The effect of age on adult red fox body weights. Prairie Nat. 13: 97-98.

Asdell, S. A. (1946) Patterns of mammalian reproduction. Ithaca, NY: Comstock Publ. Co.

Boddington, M. J. (1978) An absolute metabolic scope for activity. J. Theor. Biol. 75: 443-449.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Cook, D. B.; Hamilton, W. J., Jr. (1944) The ecological relationship of red fox food in eastern New York. Ecology 24: 94-104.

Dalke, P. D.; Sime, P. R. (1938) Home and seasonal ranges of the eastern cottontail in Connecticut. Trans. N. Amer. Wildl. Conf. 3: 659-669.

Dekker, D. (1983) Denning and foraging habits of red foxes, *Vulpes vulpes*, and their interaction with coyotes, *Canis latrans*, in central Alberta. Can. Field-Nat. 97: 303-306.

Eadie, W. R. (1943) Food of the red fox in southern New Hampshire. J. Wildl. Manage. 7: 74-77.

Green, J. S.; Flinders, J. T. (1981) Diets of sympatric red foxes and coyotes in southeastern Idaho. Great Basin Nat. 41: 251-254.

Halpin, M. A.; Bissonette, J. A. (1983) Winter resource use by red fox (*Vulpes vulpes*) (abstract only). Trans. Northeast Sect. Wildl. Soc. 40: 158.

Hamilton, W. J., Jr. (1935) Notes on food of red foxes in New York and New England. J. Mammal. 16: 16-21.

Harris, S. (1979) Age-related fertility and productivity in red foxes, *Vulpes vulpes*, in suburban London. J. Zool. (London) 187: 195-199.

Harris, S.; Smith, G. C. (1987) Demography of two urban fox (*Vulpes vulpes*) populations. J. Appl. Ecol. 24: 75-86.

Hockman, J. G.; Chapman, J. A. (1983) Comparative feeding habits of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargentus*) in Maryland. Am. Midl. Nat. 110: 276-285.

Hoffman, R. A.; Kirkpatrick, C. M. (1954) Red fox weights and reproduction in Tippecanoe County, Indiana. J. Mammal. 55: 504-509.

Johnson, W. J. (1970) Food habits of the red fox in Isle Royale National Park, Lake Superior. Am. Midl. Nat. 84: 568-572.

Johnson, D. H.; Sargeant, A. B. (1977) Impact of red fox predation on the sex ratio of prairie mallards. Washington, DC: U.S. Fish Wildl. Serv.; Wildl. Res. Rep. 6.

Jones, D. M.; Theberge, J. B. (1982) Summer home range and habitat utilization of the red fox (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargentus*) in Maryland. Am. Midl. Nat. 110: 276-285.

Keenan, R. J. (1981) Spatial use of home range among red foxes (*Vulpes vulpes*) in south-central Ontario. In: Chapman, J. A.; Pursley, D., eds. Worldwide furbearer conference proceedings, August, 1980; Frostburg, Maryland; pp. 1041-1063.

Knable, A. E. (1970) Food habits of the red fox (*Vulpes fulva*) in Union County, Illinois. Trans. Ill. State Acad. Sci. 63: 359-365.

Knable, A. E. (1974) Seasonal trends in the utilization of major food groups by the red fox (*Vulpes fulva*) in Union County, Illinois. Trans. Ill. State Acad. Sci. 66: 113-115.

Korschgen, L. J. (1959) Food habits of the red fox in Missouri. J. Wildl. Manage. 23: 168-176.

Kuehn, D. W.; Berg, W. E. (1981) Notes on movements, population statistics, and foods of the red fox in north-central Minnesota. Minn. Wildl. Res. Q. 41: 1-10.

Layne, J. N.; McKeon, W. H. (1956) Some aspects of red fox and gray fox reproduction in New York. N.Y. Fish and Game J. 3: 44-74.

Lindstrom, E. (1981) Reliability of placental scar counts in the red fox (*Vulpes vulpes* L.) with special reference to fading of the scars. Mammal Rev. 11: 137-49.

Llewellyn, L. M.; Uhler, F. M. (1952) The foods of fur animals of the Patuxent Research Refuge, Maryland. Am. Midl. Nat. 48: 193-203.

MacDonald, D. W. (1980) Social factors affecting reproduction amongst red foxes (*Vulpes vulpes* L. 1758). In: Zimen, E., ed. The red fox, biogeographica: v. 18. The Netherlands: W. Junk, The Hague; pp. 123-175.

MacDonald, D. W.; Voigt, D. R. (1985) The biological basis of rabies models. In: Bacon, P. J., ed. Population dynamics of rabies in wildlife. London, UK: Academic Press; pp. 71-107.

MacGregor, A. E. (1942) Late fall and winter foods of foxes in central Massachusetts. J. Wildl. Manage. 6: 221-224.

Major, J. T.; Sherburne, J. A. (1987) Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51: 606-616.

Maurel, D. (1980) Home range and activity rhythm of adult male foxes during the breeding season. In: Amlaner, C. J.; MacDonald, D. W., eds. A handbook on biotelemetry and radio tracking. Edmonds, WA: The Franklin Press; pp. 697-702.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Mono. 57: 111-128.

Nowak, R. M.; Paradiso, J. L. (1983) Foxes. In: Walker's mammals of the world. 4th ed. Baltimore, MD: Johns Hopkins University Press; pp. 932-980.

Palmer, E. L.; Fowler, H. S. (1975) Fieldbook of natural history. New York, NY: McGraw-Hill Book Co.

Phillips, R. L.; Andrews, R. D.; Storm, G. L.; et al. (1972) Dispersal and mortality of red foxes. J. Wildl. Manage. 36: 237-248.

Pils, C. M.; Martin, M. A. (1978) Population dynamics, predator-prey relationships and management of the red foxes in Wisconsin. Madison, WI: Wisc. Dept. Nat. Resour. Tech. Bull. No. 105; 56 pp.

Pils, C. M.; Martin, M. A.; Lange, E. (1981) Harvest, age structure, survivorship, productivity of red foxes in Wisconsin. Madison, WI: Wisc. Dept. Nat. Resour. Tech. Bull. No. 125; 19 pp.

Powell, D. G.; Case, R. M. (1982) Food habits of the red fox in Nebraska. Trans. Nebr. Acad. Sci. and Affil. Soc. 10: 13-16.

Preston, E. M. (1975) Home range defense in the red fox, *Vulpes vulpes* L. J. Mammal. 56: 645-652.

Richards, S. H.; Hine, R. L. (1953) Wisconsin fox populations. Madison, WI: Wisc. Cons. Dept. Tech. Wildl. Bull. No. 6; 78 pp.

Samuel, D. E.; Nelson, B. B. (1982) Foxes. In: Chapman, J. A.; Feldhammer, G. A., eds. Wild mammals of North America. Baltimore, MD: Johns Hopkins University Press; pp. 475-490.

Sargeant, A. B. (1972) Red fox spatial characteristics in relation to waterfowl predation. J. Wildl. Manage. 36: 225-236.

Sargeant, A. B. (1978) Red fox prey demands and implications to prairie duck production. J. Wildl. Manage. 42: 520-527.

Sargeant, A. B.; Pfeifer, W. K.; Allen, S. H. (1975) A spring aerial census of red foxes in North Dakota. J. Wildl. Manage. 39: 30-39.

Sargeant, A. B.; Allen, S. H.; Fleskes, J. P. (1986) Commercial sunflowers: food for red foxes in North Dakota. Prairie Nat. 18: 91-94.

Sargeant, A. B.; Allen, S. H.; Hastings, J. O. (1987) Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51: 285-293.

Sargeant, A. B.; Allen, S. H.; Johnson, D. H. (1981) Determination of age and whelping dates of live red fox pups. J. Wildl. Manage. 45: 760-765.

Schoonmaker, W. J. (1938) Notes on mating and breeding habits of foxes in New York state. J. Mammal. 19: 375-376.

Scott, T. G. (1943) Some food coactions of the northern plains red fox. Ecol. Monogr. 13: 427-480.

Sheldon, W. G. (1949) Reproductive behavior of foxes in New York state. J. Mammal. 30: 236-246.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Stanley, W. C. (1963) Habits of the red fox in northeastern Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Pub. 34: 1-31.

Storm, G. L.; Ables, E. D. (1966) Notes on newborn and fullterm wild red foxes. J. Mammal. 47: 116-118.

Storm, G. L.; Andrews, R. D.; Phillips, R. L.; et al. (1976) Morphology, reproduction, dispersal and mortality of midwestern red fox populations. Wildl. Monogr. 49: 1-82.

Switzenberg, D. F. (1950) Breeding productivity in Michigan red foxes. J. Mammal. 31: 194-195.

Tullar, B. J. (1983) An unusually long-lived red fox. N.Y. Fish Game J. 30: 227.

Tullar, B. J., Jr.; Berchielli, L. T. (1980) Movement of the red fox in central New York. N.Y. Fish Game J. 27: 197-204.

Vogtsberger, L. M.; Barrett, G. W. (1973) Bioenergetics of captive red foxes. J. Wildl. Manage. 37: 495-500.

Voigt, D. R.; MacDonald, D. W. (1984) Variation in the spatial and social behaviour of the red fox, *Vulpes vulpes.* Acta Zool. Fenn. 171: 261-265.

Voigt, D. R.; Tinline, R. L. (1980) Strategies for analyzing radio tracking data. In: Amlaner, C. J., Jr.; MacDonald, D. W., eds. A handbook on biotelemetry and radio tracking. Oxford, United Kingdom: Pergamon Press; pp. 387-404.

Voigt, D. (1987) Red fox. In: Novak, M.; Baker, J. A.; Obbarel, M. E.; et al., eds. Wild furbearer management and conservation. Pittsburgh, PA: University of Pittsburgh Press; pp. 379-392.

Voigt, D. R.; Broadfoot, J. (1983) Locating pup-rearing dens of red foxes with radio-equipped woodchucks. J. Wildl. Manage. 47: 858-859.

2.2.3. Raccoon (raccoons, coatis, ringtails)

<u>Order *Carnivora*, Family *Procyonidae*</u>. Procyonids are medium-sized omnivores that range throughout much of North America. Raccoons, coatis, and ringtails feed on insects, small mammals, birds, lizards, and fruits. Ringtails are much smaller and more slender than raccoons and consume a higher proportion of animal matter (Kaufmann, 1982). Coatis are slightly smaller than racoons and are limited in their distribution in the United States to just north of the Mexican border.

Selected species

The raccoon (*Procyon lotor*) is the most abundant and widespread medium-sized omnivore in the North America. They are found throughout Mexico, Central America, the United States, except at the higher elevations of the Rocky Mountains, and into southern Canada (Kaufmann, 1982). During the last 50 years, raccoon populations in the United States have increased greatly (Sanderson, 1987). In suburban areas, they frequently raid garbage cans and dumps. Raccoons are preyed on by bobcats, coyotes, foxes, and great horned owls (Kaufmann, 1982). Twenty-five subspecies are recognized in the United States and Canada; however, most researchers do not identify the subspecies studied because different subspecies inhabit essentially nonoverlapping geographic ranges.

***Body size*. Raccoons measure from 46 to 71 cm with a 20 to 30 cm tail. Body weights vary by location, age, and sex from 3 to 9 kg (Kaufmann, 1982; Sanderson, 1987). The largest raccoons recorded are from Idaho and nearby states, while the smallest reside in the Florida Keys (Lotze and Anderson, 1979). Juveniles do not reach adult size until at least the end of their second year (Stuewer, 1943b). In the autumn, fat reserves account for 20 to 30 percent or more of the raccoon's weight (Whitney and Underwood, 1952, cited in Kaufmann, 1982). In Minnesota, Mech et al. (1968) found that juveniles gained weight almost linearly until mid-November, after which they began to lose weight until April. Weight loss in adults and yearlings can reach 50 percent during the 4 months of winter dormancy (e.g., 4.3-kg loss for a 9.1-kg raccoon) (Thorkelson and Maxwell, 1974; Mech et al., 1968). In Alabama, where raccoons are active all year, winter weight losses are less, 16 to 17 percent on average (Johnson, 1970).**

***Habitat*. Raccoons are found near virtually every aquatic habitat, particularly in hardwood swamps, mangroves, floodplain forests, and freshwater and saltwater marshes (Kaufmann, 1982). They are also common in suburban residential areas and cultivated and abandoned farmlands (Kaufmann, 1982) and may forage in farmyards (Greenwood, 1982). Stuewer (1943a) stated that a permanent water supply, tree dens, and available food are essential. Raccoons use surface waters for both drinking and foraging (Stuewer, 1943a).**

***Food habits*. The raccoon is an omnivorous and opportunistic feeder. Although primarily active from sunset to sunrise (Kaufmann, 1982; Stuewer, 1943a), raccoons will change their activity period to accommodate the availability of food and water (Sanderson, 1987). For example, salt marsh raccoons may become active during the day to take advantage of low tide (Ivey, 1948, cited in Sanderson, 1987). Raccoons feed primarily on fleshy fruits, nuts, acorns, and corn (Kaufmann, 1982) but also eat grains, insects, frogs,**

crayfish, eggs, and virtually any animal and vegetable matter (Palmer and Fowler, 1975). The proportion of different foods in their diet depends on location and season, although plants are usually a more important component of the diet. They may focus on a preferred food, such as turtle eggs, when it is available (Stuewer, 1943a). They also will feed on garbage and carrion. Typically, it is only in the spring and early summer that raccoons eat more animal than plant material. Their late summer and fall diets consist primarily of fruits. In winter, acorns tend to be the most important food, although raccoons will take any corn or fruits that are still available (Kaufmann, 1982; Stuewer, 1943a).

***Temperature regulation and molt*. From the central United States into Canada, raccoons undergo a winter dormancy lasting up to 4 months (Stuewer, 1943a). It is not a true hibernation, however, and they can be easily awakened (Kaufmann, 1982). Animals in the south are active year-round (Goldman, 1950). Snow cover, more than low temperatures, triggers winter dormancy (Stuewer, 1943a; Mech et al., 1966; Kaufmann, 1982). The raccoon's annual molt begins early in spring and lasts about 3 months (Kaufmann, 1982).**

***Breeding activities and social organization.* Although solitary, adult raccoons come together for a short time during the mating period (Kaufmann, 1982), which begins earlier (January to March) in their northern range than in their southern range (March to June) (Johnson, 1970; Sanderson, 1987). Male and female home ranges overlap freely and each male may mate with several females during the breeding season (Mech et al., 1966; Johnson, 1970; Kaufmann, 1982; Stuewer, 1943a). The most common group of raccoons is a mother and her young of that year. Further north in their range, a family will den together for the winter and break up the following spring (Kaufmann, 1982). Males are territorial toward one another but not toward females; females are not territorial (Fritzell, 1978).**

***Home range and resources*. The size of a raccoon's home range depends on its sex and age, habitat, food sources, and the season (Sanderson, 1987). Values from a few hectares to more than a few thousand hectares have been reported, although home ranges of a few hundred hectares appear to be most common (see Appendix). In general, home ranges of males are larger than those of females, the home range of females with young is restricted, and winter ranges are smaller than ranges at other times of the year for both sexes (Sanderson, 1987). During the winter, raccoons commonly den in hollow trees; they also use the burrows of other animals such as foxes, groundhogs, skunks, and badgers. These sites are used for sleeping during warmer periods. After wintering in one den, the female will choose a new den in which to bear her young (Kaufmann, 1982). Schneider et al. (1971) found that once the cubs leave the den, the family will not use it again that year.**

***Population density*. Population density depends on the quality and quantity of food resources and den sites. Values between 0.005 and 1.5 raccoons per hectare have been reported, although 0.1 to 0.2 per hectare is more common (see Appendix). Populations exceeding one raccoon per hectare have been reported in residential areas (Hoffman and Gottschang, 1977). Although raccoons may prefer tree dens over ground dens, particularly for raising young (Stuewer, 1943a), Butterfield (1954) found high raccoon densities in an area with few tree dens but numerous ground dens.**

Population dynamics. **Males generally are not sexually mature by the time of the first regular breeding season following their birth, but they may mature later that summer or fall (Johnson, 1970; Sanderson, 1951). Females may become pregnant in their first year (Johnson, 1970). In a review of several studies, Kaufmann (1982) found that up to 60 percent of both wild and captive females mate and produce litters in their first year. In Illinois and Missouri, Fritzell et al. (1985) found pregnancy rates of yearlings from 38 to 77 percent. After their first year, almost all females breed annually (Fritzell et al., 1985). Females produce only one litter each year, and the female alone cares for the young (Sanderson, 1987; Stuewer, 1943a, 1943b). With some exceptions (Bissonnette and Csech, 1937), larger litter sizes usually occur in the raccoon's northern range (Lotze and Anderson, 1979). Some juveniles of both sexes disperse from the areas where they were born during the fall or winter of their first year, while others stay and raise young within their parents' home range (Stuewer, 1943a). The highest mortality rates occur within the first 2 years; the age structure of populations in Alabama suggests that mortality is higher for subadults than for juveniles (Johnson, 1970).**

Similar species (from general references)

- **The coati (*Nasua nasua*) is slightly smaller than the raccoon (4 to 6 kg) but with a much longer tail (51 to 64 cm). Ranging throughout Central America from Panama to Mexico (Kaufmann, 1982), the coati is rare in the United States where it inhabits open forests of the southwest, near the Mexican border. It forages primarily for grubs and tubers but also feeds on fruits, nuts, bird eggs, lizards, scorpions, and tarantulas. Coatis roll arthropods on the ground to remove wings and scales.**

- **The ringtail (*Bassariscus astutus*) is smaller (36 to 41 cm; 0.9 to 1.13 kg) than the raccoon, with a tail equal to its body length. It ranges throughout the southwestern United States into northern California and Oregon, inhabiting chaparral, rocky ridges, and cliffs near water. Ringtails are omnivorous like the raccoon but consume a higher proportion of animal matter, feeding mainly on small mammals, insects, birds, and lizards as well as fruits. They den in caves or crevices along cliffs, hollow trees, under rocks, and in unused buildings. Although ringtails sometimes live in colonies, mated pairs are more common. More nocturnal than the raccoon, the ringtail is only active at dawn and dusk (Kaufmann, 1982).**

General references

Burt and Grossenheider (1980); Goldman (1950); Johnson (1970); Kaufmann (1982); Palmer and Fowler (1975); Sanderson (1987).

Raccoon (*Procyon lotor*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI)	Location	Reference	Note No.
Body Weight (kg)	A M	7.6	7.0 - 8.3	wc Illinois	Sanderson, 1984	
	A F parous	6.4	5.6 - 7.1			
	A F nulliparous	6.0	5.1 - 7.1			
	J M	5.1	4.6 - 5.7			
	J F	4.8	4.2 - 5.3			
	A M	6.76		Missouri	Nagel, 1943	
	A F	5.74				
	A M	4.31	up to 8.8	Alabama	Johnson, 1970	
	A F	3.67	up to 5.9			
	neonate	0.075		w New York/captive	Hamilton, 1936	
Pup Growth Rate (g/day)	birth to 7 days	17		w New York	Hamilton, 1936	
	8 to 19 days	21				
	20 to 30 days	11				
	31 to 40 days	12				
	41 to 50 days	23				
	birth to 6 wks	17.8		NS/lab	Montgomery, 1969	
	6 to 9 wks	3.9				
	10 to 16 wks	29.5				
Metabolic Rate (lO_2/kg-day)	Winter 15-35°C	9.36 ± 1.68 SD		Washington, DC/National Zoo	Mugaas et al., 1984	
Metabolic Rate (kcal/kg-day)	J B	304		Ohio/lab	Teubner & Barrett, 1983	
	A M basal	44.8			estimated	1
	A F basal	46.8				
	A M free-living	183	(83 - 400)		estimated	2
	A F free-living	187	(85 - 408)			
Food Ingestion Rate (g/g-day)						3

Raccoon (*Procyon lotor*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI)	Location	Reference	Note No.
Water Ingestion Rate (g/g-day)	A M A F	0.082 0.083			estimated	4
Inhalation Rate (m^3/day)	A M A F	2.47 2.17			estimated	5
Surface Area (cm^2)	A M A F	3,796 3,414			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
crayfish	37	8	3	9	Maryland/forested bottomland	Llewellyn & Uhler, 1952	
snails	5	5	3	6			
insects	40	39	18	12	(% wet volume; digestive tract)		
reptiles/amphibians	6	5	3	7			
fish	3	2	trace	2			
rodents	7	2	trace	8			
corn	0	1	2	19			
Smilax	0	trace	trace	6			
acorns	0	trace	5	17			
pokeberry	0	trace	17	2			
wild cherry	0	17	2	0			
blackberries	0	16	trace	0			
grapes	0	trace	23	8			
persimmon	0	0	11	7			

Raccoon (*Procyon lotor*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
frogs	8.1	trace	0	0	Tennessee/NS	Tabatabai & Kennedy, 1988	
fish	1.2	0	0	0			
birds	trace	0	trace	8.4	(% wet volume; digestive tract)		
mammals	1.7	0	1.4	0			
other/unspecified	7.8	6.7	1.8	7.2			
persimmon	0	35.8	57.3	27.4			
corn	57.6	0	10.0	25.9			
grapes	0	trace	10.2	0			
pokeberry	0	20.5	4.5	0			
acorns	0	0	5.4	4.2			
sugar hackberry	0	0	5.5	18.4			
cherry	0	29.5	0	0			
insects	22.0	3.5	2.4	trace			
crayfish	1.6	4.0	1.5	1.4			
Mollusca (mussels and oysters)		44			sw Washington/tidewater mudflats	Tyson, 1950	
Crustacea (shrimp & crabs)		25			(% wet volume; stomach contents)		
Pisces (goby & cabezon)		9					
Annelida (marine worms)		20					
Echiurida (worm)		1					
fruits		37.9			New York/NS	Hamilton, 1951	7
insects		8.2					
mammals		14.3			(% wet volume; stomach contents)		
grains (e.g. corn)		14.7					
earthworms		7.2					
amphibians		4.4					
vegetation		6.1					
reptiles		3.0					
molluscs		1.9					
birds		1.5					
carrion		1.5					
unspecified		0.2					

Raccoon (*Procyon lotor*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A M spr./sum. A F spr./sum.	2,560 806	670 - 4,946 229 - 1,632	North Dakota/prairie potholes	Fritzell, 1978	8
	A M May - Dec A F May - Dec	204 108	18.2 - 814 5.3 - 376	Michigan/riparian	Stuewer, 1943a	
	A M all year A F all year	65 ± 18 SE 39 ± 16 SE		Georgia/coastal island	Lotze, 1979	9
Population Density (N/ha)	NS	1.46		Ohio/residential woods	Hoffman & Gottschang, 1977	
	spring	0.17		Lake Erie, Ohio/ Sandusky Bay, marsh	Urban, 1970	10
	spring	0.022		Wisconsin/marsh	Dorney, 1954	
Litter Size	1 to 3 yrs 4 yrs +	3.4 3.8		n Illinois/NS	Fritzell et al., 1985	
		2.43		Alabama/bottomlands, marsh	Johnson, 1970	
Litters /Year		1		most of range/NS	Sanderson, 1987	
Days Gestation		63		North America/NS	Hamilton, 1936; Sanderson, 1987; Stuewer, 1943b	
Age at Weaning (days)		84	63 - 112	NS/lab	Montgomery, 1969	
Age at Sexual Maturity	M	15 months		Alabama/NS	Johnson, 1970	
	F	1 year		IL, MO/NS	Fritzell et al., 1985	
Annual Mortality Rates (percent)	A B	56		Missouri/NS	Sanderson, 1951	11
	A B J B	38 42		sw Iowa/agricultural	Clark et al., 1989	

Raccoon (*Procyon lotor*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Longevity	A B A B	3.1 years 1.8 years		Alabama/NS Missouri/NS	Johnson, 1970 Sanderson, 1951	 11

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	February January	March February	August March	sw Georgia, nw Florida n United States	McKeever, 1958 Johnson, 1970	
Parturition	April April	early April May	May October	Michigan sw Georgia, nw Florida	Stuewer, 1943b McKeever, 1958	
Molt		summer		northern latitudes	Goldman, 1950	
Torpor	late November		March/April	ec Minnesota	Whitney & Underwood, 1952	12

1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Nagel (1943).
2 Estimated using equation 3-45 (Nagy, 1987) and body weights from Nagel (1943).
3 See Chapters 3 and 4 for methods for calculating food ingestion rates from free-living metabolic rate and diet.
4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Nagel (1943).
5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Nagel (1943).
6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Nagel (1943).
7 Collections from April through October.
8 Measured from April through July.
9 Based on radiotracking.
10 Average of three methods of estimating density.
11 Hunted population.
12 Cited in Schneider et al. (1971).

References (including Appendix)

Alexander, G. (1977) Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10: 181-195.

Arthur, S. C. (1928) The fur animals of Louisiana. Louisiana Dept. Conserv.; Bull. No. 18.

Asdell, S. A. (1964) Patterns of mammalian reproduction. Ithaca, NY: Comstock Publ. Co.

Bailey, V. (1936) The mammals and life zones of Oregon. U.S. Dept. Agr., Bur. Biol. Survey, North Am. Fauna 55: 1-416.

Bissonnette, T. H.; Csech, A. G. (1937) Modification of mammalian sexual cycles. Part 7, fertile matings of raccoons in December instead of February induced by increasing daily periods of light. Proc. R. Soc. London, ser. B 827: 246-254.

Boddington, M. J. (1978) An absolute metabolic scope for activity. J. Theor. Biol. 75: 443-449.

Brown, C. E. (1936) Rearing wild animals in captivity, and gestation periods. J. Mammal. 17: 10-13.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Butterfield, R. T. (1944) Populations, hunting pressure, and movement of Ohio raccoons. Trans. North Am. Wildl. Conf. 9: 337-344.

Butterfield, R. T. (1954) Some raccoon and groundhog relationships. J. Wildl. Manage. 18: 433-437.

Cagle, F. R. (1949) Notes on the raccoon, *Procyon lotor megalodous* Lowery. J. Mammal. 30: 45-47.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Cauley, D. L.; Schinner, J. R. (1973) The Cincinnati raccoons. Nat. Hist. 82: 58-60.

Clark, W. R.; Hasbrouck, J. J.; Kienzler, J. M.; et al. (1989) Vital statistics and harvest of an Iowa raccoon population. J. Wildl. Manage. 53: 982-990.

Cowan, W. F. (1973) Ecology and life history of the raccoon (*Procyon lotor hirtus* Nelson and Goldman) in the northern part of its range [Ph.D. dissertation]. Grand Forks, ND: University of North Dakota.

Cunningham, E. R. (1962) A study of the eastern raccoon, *Procyon lotor* (L.), on the Atomic Energy Commission Savannah River Plant [master's thesis]. Athens, GA: University of Georgia.

Dew, R. D. (1978) Biology of the raccoon, *Procyon lotor*; I. Genic variation. II. Population age structure and average litter size [master's thesis]. Memphis, TN: Memphis State University.

Dorney, R. S. (1954) Ecology of marsh raccoons. J. Wildl. Manage. 18: 217-225.

Eisenberg, J. F. (1981) The mammalian radiations; an analysis of trends in evolution, adaptation, and behavior. Chicago, IL: University of Chicago Press.

Ewer, R. F. (1973) The carnivores. Ithaca, NY: Cornell University Press.

Flower, S. S. (1931) Contributions to our knowledge of the duration of life in vertebrate animals. V. Mammals. Zool. Soc. London. Proc. (part 1): 145-234.

Fritzell, E. K. (1978) Habitat use by prairie raccoons during the waterfowl breeding season. J. Wildl. Manage. 42: 118-127.

Fritzell, E. K.; Hubert, G. F., Jr.; Meyen, B. E.; et al. (1985) Age-specific reproduction in Illinois and Missouri raccoons. J. Wildl. Manage 49: 901-905.

Goldman, E. A. (1950) Raccoons of North and Middle America. Washington, DC: U.S. Fish Wildl. Serv.; North Am. Fauna 60.

Greenwood, R. J. (1982) Nocturnal activity and foraging of prairie raccoons (*Procyon lotor*) in North Dakota. Am. Midl. Nat. 107: 238-243.

Hamilton, W. J., Jr. (1936) The food and breeding habits of the raccoon. Ohio J. Sci. 36: 131-140.

Hamilton, W. J., Jr. (1940) The summer food of minks and raccoons on the Montezuma Marsh, New York. J. Wildl. Manage. 4: 80-84.

Hamilton, W. J., Jr. (1951) Warm weather foods of the raccoon in New York state. J. Mammal. 32: 341-344.

Hoffman, C. O.; Gottschang, J. L. (1977) Numbers, distribution, and movements of a raccoon population in a suburban residential community. J. Mammal. 58: 623-636.

Ivey, R. D. (1948) The raccoon in the salt marshes of northeastern Florida. J. Mammal. 29: 290-291.

Johnson, A. S. (1970) Biology of the raccoon (*Procyon lotor varius* Nelson and Goldman) in Alabama. Alabama Cooperative Wildlilfe Research Unit; Auburn Univ. Agric. Exp. Stn. Bull. 402.

Kaufmann, J. H. (1982) Raccoon and allies. In: Chapman, J. A.; Feldhamer, G. A., eds. Wild mammals of North America. Baltimore, MD: Johns Hopkins University Press; pp. 567-585.

Llewellyn, L. M.; Uhler, F. M. (1952) The foods of fur animals of the Patuxent Research Refuge, Maryland. Am. Midl. Nat. 48: 193-203.

Lotze, J.-H. (1979) The raccoon (*Procyon lotor*) on St. Catherines Island, Georgia. 4. Comparisons of home ranges determined by livetrapping and radiotracking. New York, NY: American Museum of Natural History; Rep. No. 2664.

Lotze, J.-H.; Anderson, S. (1979) *Procyon lotor*. American Society of Mammalogists; Mammalian Species No. 119.

Lowery, G. H., Jr. (1936) A preliminary report on the distribution of the mammals of Louisiana. Louisiana Acad. Sci. Proc. 3: 1-39.

McComb, W. C. (1981) Effects of land use upon food habits, productivity, and gastrointestinal parasites of raccoons. In: Chapman, J. A.; Pursley, D., eds. Proceedings worldwide furbearer conference: v. 1, August 1980; Frostburg, MD; pp. 642-651.

McKeever, S. (1958) Reproduction in the raccoon in the southeastern United States. J. Wildl. Manage. 22: 211.

Mech, L. D.; Tester, J. R.; Warner, D. W. (1966) Fall daytime resting habits of raccoons as determined by telemetry. J. Mammal. 47: 450-466.

Mech, L. D.; Barnes, D. M.; Tester, J. R. (1968) Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. J. Mammal. 49: 63-73.

Montgomery, G. G. (1969) Weaning of captive raccoons. J. Wildl. Manage. 33: 154-159.

Moore, D. W.; Kennedy, M. L. (1985) Weight changes and population structure of raccoons in western Tennessee. J. Wildl. Manage. 49: 906-909.

Mugaas, J. N.; Mahlke, K. P.; Broudy, E.; et al. (1984) Metabolism of raccoons, *Procyon lotor*, in winter and summer (abstract only). Am. Zool. 24: 89A.

Nagel, W. O. (1943) How big is a 'coon. Missouri Conservationist 6-7.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Mono. 57: 111-128.

Palmer, E. L.; Fowler, H. S. (1975) Fieldbook of natural history. New York, NY: McGraw-Hill Book Co.

Sanderson, G. C. (1951) Breeding habits and a history of the Missouri raccoon population from 1941 to 1948. Trans. North Am. Wildl. Conf. 16: 445-461.

Sanderson, G. C. (1984) Cooperative raccoon collections. Ill. Nat. Hist. Survey Div.; Pittman-Robertson Proj. W-49-R-31.

Sanderson, G. C. (1987) Raccoon. In: Novak, M.; Baker, J. A.; Obbarel, M. E.; et al., eds. Wild furbearer management and conservation. Pittsburgh, PA: University of Pittsburgh Press; pp. 487-499.

Sanderson, G. C.; Hubert, G. F. (1981) Selected demographic characteristics of Illinois (U.S.A.) raccoons (*Procyon lotor*). In: Chapman, J. A.; Pursley, D., eds. Worldwide furbearer conference proceedings: v. 1. August 1980; Frostburg, Maryland.

Sanderson, G. C.; Nalbandov, A. V. (1973) The reproductive cycle of the raccoon in Illinois. Illinois Nat. Hist. Surv. Bull. 31: 29-85.

Schneider, D. G.; Mech, D. L.; Tester, J. R. (1971) Movements of female raccoons and their young as determined by radio-tracking. Anim. Behav. Monogr. 4: 1-43.

Schoonover, L. J.; Marshall, W. H. (1951) Food habits of the raccoon (*Procyon lotor hirtus*) in north-central Minnesota. J. Mammal. 32: 422-428.

Seton, E. T. (1929) Lives of game animals. Garden City, NJ: Doubleday, Doran and Company.

Sherfy, F. C.; Chapman, J. A. (1980) Seasonal home range and habitat utilization of raccoons in Maryland. Carnivore 3: 8-18.

Slate, D. (1980) A study of New Jersey raccoon populations--determination of the densities, dynamics and incidence of disease in raccoon populations in New Jersey. N.J. Div. Fish, Game, and Wildl.; Pittman-Robertson Proj. W-52-R-8, Final Rep.

Sonenshine, D. E.; Winslow, E. L. (1972) Contrasts in distribution of raccoons in two Virginia localities. J. Wildl. Manage. 36: 838-847.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Stains, H. J. (1956) The raccoon in Kansas: natural history, management, and economic importance. Univ. Kansas Mus. Nat. Hist., Misc. Publ. 10: 1-76.

Stuewer, F. W. (1943a) Raccoons: their habits and management in Michigan. Ecol. Monogr. 13: 203-257.

Stuewer, F. W. (1943b) Reproduction of raccoons in Michigan. J. Wildl. Manage. 7: 60-73.

Tabatabai, F. R.; Kennedy, M. L. (1988) Food habits of the raccoon (*Procyon lotor*) in Tennessee. J. Tenn. Acad. Sci. 63: 89-94.

Tester, J. R. (1953) Fall food habits of the raccoon in the South Platte Valley of northeastern Colorado. J. Mammal. 34: 500-502.

Teubner, V. A.; Barrett, G. W. (1983) Bioenergetics of captive raccoons. J. Wildl. Manage. 47: 272-274.

Thorkelson, J.; Maxwell, R. K. (1974) Design and testing of a heat transfer model of a raccoon *(Procyon lotor)* in a closed tree den. Ecology 55: 29-39.

Tyson, E. L. (1950) Summer food habits of the raccoon in southwest Washington. J. Mammal. 31: 448-449.

Urban, D. (1970) Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. J. Wildl. Manage. 34: 372-382.

VanDruff, L. W. (1971) The ecology of the raccoon and opossum, with emphasis on their role as waterfowl nest predators [Ph.D. dissertation]. Ithaca, NY: Cornell University.

Whitney, L. F.; Underwood, A. B. (1952) The raccoon. Orange, CT: Practical Science Publ.

Wood, J. E. (1954) Food habits of furbearers of the upland post oak region in Texas. J. Mammal. 35: 406-415.

Yeager, L. E.; Rennels, R. G. (1943) Fur yield and autumn foods of the raccoon in Illinois river bottom lands. J. Wildl. Manage. 7: 45-60.

2.2.4. Mink (mink, weasels, ermine)

Order *Carnivora*, Family *Mustelidae*. Although varied in size, most members of this family have long, slender bodies and short legs. Throughout the family, the male is usually larger than the female. The more terrestrial species feed primarily on small mammals and birds. Mustelids that live around lakes and streams feed on aquatic prey such as fish, frogs, and invertebrates (Burt and Grossenheider, 1980).

Selected species

The mink (*Mustela vison*) is the most abundant and widespread carnivorous mammal in North America. Mink are distributed throughout North America, except in the extreme north of Canada, Mexico, and arid areas of the southwestern United States. It is common throughout its range but often overlooked because of its solitary nature and nocturnal activity. Mink are particularly sensitive to PCBs and similar chemicals, and have been found to accumulate PCBs in subcutaneous fat to 38 to 200 times dietary concentrations, depending on the PCB congener (Hornshaw et al., 1983).

Body size. **Body size varies greatly throughout the species' range, with males weighing markedly more than females (in some populations, almost twice as much, see table). Males measure from 33 to 43 cm with a 18 to 23 cm tail. Females measure from 30 to 36 cm with a 13 to 20 cm tail (Burt and Grossenheider, 1980). Farm-raised mink tend to be larger than wild mink (letter from R.J. Aulerich, Department of Animal Science, Michigan State University, East Lansing, MI, to Susan Norton, January 7, 1992).**

Metabolism**. Harper et al. (1978) evaluated the energy requirements of growing farm-raised male mink during a 21-day period when about 20 percent of their total growth would occur. They expressed food intake on the basis of metabolic body size (MBS) instead of body weight (BW) where MBS = $BW(kg)^{0.73}$. Metabolizable energy (ME) requirements were 147.8 ± 6.06 ($kcal/kg_{MBS}$-day). Accounting for assimilation efficiency, this corresponded to a gross energy (GE) intake of approximately 203 ($kcal/kg_{MBS}$-day).**

Iversen (1972) found that basal metabolic rate for mink and other mustelids weighing 1 kg or more could be expressed by the equation:

$$BMR = 84.6Wt^{0.78} (\pm 0.15),$$

where BMR = basal metabolic rate in kcal/day and Wt = body weight in kilograms. This model reflects the finding that the larger mustelids have a slightly (10 to 15 percent) higher basal metabolic rate than expected for mammals in general.[f] Free-living metabolic rates would be expected to be three to five times higher (see table).

Habitat**. Mink are found associated with aquatic habitats of all kinds, including waterways such as rivers, streams, lakes, and ditches, as well as swamps, marshes, and**

---

[f]Mustelid species much smaller than 1 kg (i.e., the stoat and weasel) have much higher basal metabolic rates than predicted for mammals in general.

backwater areas (Linscombe et al., 1982). Mink prefer irregular shorelines to more open, exposed banks (Allen, 1986). They also tend to use brushy or wooded cover adjacent to the water, where cover for prey is abundant and where downfall and debris provide den sites (Allen, 1986).

***Food habits*. Mink are predominantly nocturnal hunters, although they are sometimes active during the day. Shorelines and emergent vegetation are the mink's principal hunting areas (Arnold, 1986, cited in Eagle and Whitman, 1987). Mink are opportunistic feeders, taking whatever prey is abundant (Hamilton, 1936, 1940; Errington, 1954; Sargeant et al., 1973). Mammals are the mink's most important prey year-round in many parts of their range (Eagle and Whitman, 1987), but mink also hunt aquatic prey such as fish, amphibians, and crustaceans and other terrestrial prey such as bird, reptiles, and insects, depending on the season (Linscombe et al., 1982). In marsh habitats in summer, muskrats can be an important food source depending on their population density and vulnerability (e.g., health) (Hamilton, 1940; Sealander, 1943; Errington, 1954). Mink diet also can depend on marsh water level; Proulx et al. (1987) found that with high water levels, mink captured predominantly crayfish and meadow voles, but during periods of low water, the mink preyed on aquatic birds and muskrats deeper in the marsh. Similarly, Errington (1939) found that mink predation on muskrats in the prairie pothole region can increase dramatically in times of drought as the muskrat burrows become more exposed. Also in this region, ducklings and molting adult ducks that frequent shorelines are particularly vulnerable to mink predation (Arnold and Fritzell, 1987; Sargeant et al., 1973). In winter, mink often supplement their diet with fish (Eagle and Whitman, 1987). Females tend to be limited to smaller prey than males, who are able to hunt larger prey such as rabbits and muskrats more successfully (Birks and Dunstone, 1985; Sealander, 1943).**

***Temperature regulation and molt*. In winter, mink do not undergo hibernation or torpor; instead, they are active year-round. Mink replace their summer coat in mid to late fall with a darker more dense coat and molt again in the spring (Eagle and Whitman, 1987; Linscombe et al., 1982).**

***Breeding activities and social organization*. Mating occurs in late winter to early spring (Eagle and Whitman, 1987). Variation in the length of mating season with different subspecies reflects adaptations to different climates (Linscombe et al., 1982). Ovulation is induced by mating, and implantation is delayed (Eagle and Whitman, 1987). Parturition generally occurs in the late spring, and the mink kits are altricial (helpless) at birth (Linscombe et al., 1982). Mink are generally solitary, with females only associating with their young of the year. Female home ranges generally do not overlap with the home ranges of other females, nor do the home ranges of males overlap with each other (Eagle and Whitman, 1987). The home range of a male may overlap the home range of several females, however, particularly during the breeding season (Eagle and Whitman, 1987).**

***Home range and resources*. The home range of mink encompasses both their foraging areas around waterways and their dens. When denning, mink use bank burrows of other animals, particularly muskrats, as well as cavities in tree roots, rock or brush piles, logjams, and beaver lodges (Melquist et al., 1981; Birks and Linn, 1982; Eagle and Whitman, 1987). Individual mink may use several different dens within their home range, males more so than females (Birks and Linn, 1982). Melquist et al. (1981) found that den**

sites in Idaho were 5 to 100 m from the water, and they never observed mink more than 200 m from water. The shape of mink home ranges depends on habitat type; riverine home ranges are basically linear, whereas those in marsh habitats tend to be more circular (Birks and Linn, 1982; Eagle and Whitman, 1987). Home range size depends mostly on food abundance, but also on the age and sex of the mink, season, and social stability (Arnold, 1986; Birks and Linn, 1982; Eagle and Whitman, 1987; Linn and Birks, 1981; Mitchell, 1961). In winter, mink spend more time near dens and use a smaller portion of their home range than in summer (Gerell, 1970, cited in Linscombe et al., 1982). Adult male home ranges are generally larger than adult female home ranges (Eagle and Whitman, 1987), particularly during the mating season when males may range over 1,000 ha (Arnold, 1986).

***Population density*. Population density depends on available cover and prey. Population densities typically range from 0.01 to 0.10 mink per hectare (see table). In riverine environments, it can be more meaningful to measure densities in terms of number of mink per unit length of shoreline covered rather than in terms of number per hectare.**

***Population dynamics*. Mink reach sexual maturity at 10 months to a year and may reproduce for 7 years, possibly more (Enders, 1952; Ewer, 1973). Female mink can reproduce once per year and usually give birth to their first litters at the age of 1 year (Eagle and Whitman, 1987). Females often live to the age of 7 years in captivity (Enders, 1952).**

Similar species (from general references)

- **The long-tailed weasel (*Mustela frenata*) is smaller (males 23 to 27 cm, 200 to 340 g; females 20 to 23 cm, 85 to 200 g) than the mink. It is considered beneficial in agriculture because it kills small rodents, but it does not harm poultry. Although it does not range as far north as the mink, the long-tailed weasel does inhabit parts of the southwest.**

- **The least weasel (*Mustela nivalis*) is smaller than the mink (males 15 to 17 cm, 39 to 63 g; females 14 to 15 cm, 38 to 40 g) and inhabits meadows, fields, and wooded areas. The least weasel feeds extensively on mice and insects. Its habitat is limited to the north central United States and Canada.**

- **The ermine (*Mustela erminea*), or shorttail weasel, is smaller (males 15 to 17 cm, 71 to 170 g; females 13 to 19 cm, 28 to 85 g) than the mink. The ermine inhabits woody areas near water and feeds primarily on small mammals. The ermine's range is limited to the northern and western United States and Canada.**

- **The black-footed ferret (*Mustela nigripes*) is larger (36 to 46 cm; up to 1.1 kg) than the mink and inhabits western prairies in the United States, although it now is an endangered species. It feeds on prairie dogs and other small animals.**

General references

Burt and Grossenheider (1980); Eagle and Whitman (1987); Hall (1981); Linscombe et al. (1982); Palmer and Fowler (1975).

Mink (*Mustela vison*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Weight (g)	A M		< 2,300	western races	Harding, 1934	1
	A M		< 1,400	eastern races	Harding, 1934	1
	A M spring	1,734 ± 350 SD		Michigan (farm-raised)	Hornshaw et al., 1983	
	A F spring	974 ± 202 SD				
	A M summer	1,040		Montana	Mitchell, 1961	
	J M summer	777				
	A M fall	1,233				
	J M fall	952				
	A F summer	550		Montana	Mitchell, 1961	
	J F summer	533				
	A F fall	586				
	J F fall	582				
	neonate		6 - 10	NS	Eagle & Whitman, 1987	
	neonate	8.3 ± 1.54 SD		Michigan (farm-raised)	Hornshaw et al., 1983	
Pup Growth Rate (g/day)	0-30 days; M	7.0		NS/(farm-raised)	Wehr et al. (unpublished)	2
	31-90 d; M	21				
	91-120 d; M	15				
	121-150 d; M	9.0				
	151-180 d; M	4.3				
	0-30 days; F	6.5				
	31-90 d; F	13				
	91-120 d; F	6.7				
	121-150 d; F	1.7				
	151-180 d; F	0.6				

Mink (*Mustela vison*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Metabolic Rate (kcal/kg-day)	A F basal	96			estimated	3
	A M basal	84				
	A F ranch cage	258		(farm-raised)	Farrell & Wood, 1968b	
	A F free-living	258	(110 - 507)		estimated	4
	A M free-living	236	(121 - 550)			
Food Ingestion Rate (g/g-day)	A M summer	0.13		(captive)	Arnold & Fritzell, 1987	5
	A M winter	0.12 ± 0.0048 SE		Michigan (farm-raised)	Bleavins & Aulerich, 1981	6
	A F winter	0.16 ± 0.0075 SE				
	A M yr-round	0.22			estimated	7
Water Ingestion Rate (g/g-day)	A F	0.11			estimated	8
	A M	0.099				
	A F	0.028		(farm-raised)	Farrell & Wood, 1968c	9
Inhalation Rate (m^3/day)	A F	0.33			estimated	10
	A M	0.55				
Surface Area (cm^2)	A F	743			estimated	11
	A M	1,120				

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
ducks	5.2	32.5			Manitoba, Can/aspen parklands of prairie potholes	Arnold & Fritzell, 1987	
other birds	18.8	21.6					
eggs	3.3	14.5					
muskrats	42.0	2.1					
ground squirrels	14.2	0.5			(% dry weight in scats; male mink only)		
other mammals	15.5	25.3					
insects	1.0	3.5					

Mink (*Mustela vison*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
(habitat/season)	(stream; year-round)		(river; year-round)		Michigan/stream, river	Alexander, 1977	
trout	52		56				
non-trout fish	6		26		(% wet weight; stomach contents)		
unidentified fish	3		3				
crustaceans	11		4				
amphibians	2		3				
birds/mammals	5		6				
vegetation	17		1				
unidentified	4		1				
(sex of mink)				(M) (F)	Michigan/NS	Sealander, 1943	12
muskrat				43 14			
cottontail				16 12	(% volume; stomach contents)		
small mammals				5 17			
large birds				18 11			
small birds				trace			
snakes				2 2			
frogs				10 37			
fish				5 4			
crayfish				1 3			
frogs				24.9	Missouri/statewide	Korschgen, 1958	
mice & rats				23.9			
fish				19.9			
rabbits				10.2	(% dry volume; stomach contents)		
crayfish				9.3			
birds				5.6			
fox squirrels				2.2			
muskrats				1.3			
other				2.7			

Mink (*Mustela vison*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size			259 - 380 ha	North Dakota/prairie potholes	Eagle (unpublished)	13
	A M	770 ha		Manitoba, Canada/prairie potholes	Arnold & Fritzell, 1987	
				Montana/riverine:	Mitchell, 1961	
	A F		7.8 ha	heavy vegetation		
	A F		20.4 ha	sparse vegetation		
	A M	2.63 km	1.8 - 5.0 km	Sweden/stream	Gerell, 1970	1
	J M	1.23 km	1.1 - 1.4 km			
	A F	1.85 km	1.0 - 2.8 km			
Population Density		0.03 - 0.085 N/ha		Montana/river	Mitchell, 1961	
	A F winter	0.006 N/ha		Michigan/river	Marshall, 1936	14
	A F winter	0.6 N/km river				
Litter Size		4.2		Michigan/(farm-raised)	Hornshaw et al., 1983	
		4	2 - 8	Montana/river	Mitchell, 1961	
			4 - 10	North America/NS	Hall & Kelson, 1959	
Litters /Year		1		North America/NS	Hall & Kelson, 1959	
Days Gestation			39 - 76	North America/NS	Hall & Kelson, 1959	
		51	40 - 75	United States/(farm-raised)	Enders, 1952	
Age at Weaning	eat meat	37 days		Louisiana/NS	Svilha, 1931	14
	fully homeothermic	7 weeks		NS/NS	Kostron & Kukla, 1970	14
Age at Sexual Maturity	B	10 months		United States/(farm-raised)	Enders, 1952	
	B	1 year		NS/NS	Ewer, 1973	15
Longevity			maximum 10 years	NS/zoo	Eisenberg, 1981	
	F	7	maximum 11 years	NS/(farm-raised)	Enders, 1952	

Mink (*Mustela vison*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating		April March fall		Alaska Montana Florida, Cypress Swamp	Burns, 1964 Mitchell, 1961 Humphrey & Zinn, 1982	14
Parturition	April		June	most areas (except south)	Eagle & Whitman, 1987	
Molt		mid- to late fall		NS	Eagle & Whitman, 1987	

1 Cited in Linscombe et al. (1982).
2 Cited in NRC (1982).
3 Estimated using Iversen's (1972) model and summer body weights from Mitchell (1961); equation 3-43 (Boddington, 1978) and body weights from Mitchell (1961) yield slightly lower estimates (see text).
4 Estimated using equation 3-47 (Nagy 1987) and body weights from Mitchell (1961).
5 Arnold and Fritzell (1987) estimated that mink require 180 g of prey per day by assuming a male body mass of 1,420 g and using the model of Cowan et al. (1957) derived from measures of prey requirements for captive mink.
6 Diet of whole chicken (20 percent), commercial mink cereal (17 percent), ocean fish scraps (13 percent), and beef parts, cooked eggs, and powdered milk. Moisture content of feed = 66.2 percent.
7 Estimated using equation 3-47 (Nagy, 1987), summer body weights from Mitchell (1961), and dietary composition of Alexander (1977). See Chapter 4, Figure 4-7 for the calculations.
8 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Mitchell (1961).
9 Diet contained 65 percent water.
10 Estimated using equation 3-20 (Stahl, 1967) and body weights from Mitchell (1961).
11 Estimated using equation 3-22 (Stahl, 1967) and body weights from Mitchell (1961).
12 Collected from fur buyers.
13 Cited in Allen (1986).
14 Cited in Eagle and Whitman (1987).
15 Cited in Eisenberg (1981).

References (including Appendix)

Alexander, G. (1977) Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10: 181-195.

Allen, A. W. (1986) Habitat suitability index models: mink. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.127).

Arnold, T. W. (1986) The ecology of prairie mink during the waterfowl breeding season [master's thesis]. Columbia, MO: University of Missouri.

Arnold, T. W.; Fritzell, E. K. (1987) Food habits of prairie mink during the waterfowl breeding season. Can. J. Zool. 65: 2322-2324.

Birks, J. D.; Dunstone, N. (1985) Sex-related differences in the diet of the mink *Mustela vison*. Holarctic Ecol. 8: 245-252.

Birks, J. D.; Linn, I. J. (1982) Studies of home range of the feral mink, *Mustela vison*. Symp. Zool. Soc. Lond. 49: 231-257.

Bleavins, M. R.; Aulerich, R. J. (1981) Feed consumption and food passage in mink (*Mustela vison*) and European ferrets (*Mustela putorius furo*). Lab. Anim. Sci. 31: 268-269.

Boddington, M. J. (1978) An absolute metabolic scope for activity. J. Theor. Biol. 75: 443-449.

Burgess, S. A.; Bider, J. R. (1980) Effects of stream habitat improvements on invertebrates, trout populations, and mink activity. J. Wildl. Manage. 44: 871-880.

Burns, J. J. (1964) The ecology, economics, and management of mink in the Yukon-Kuskokwim Delta, Alaska [master's thesis]. Anchorage, AK: University of Alaska.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Chanin, P. R.; Linn, I. (1980) The diet of the feral mink (*Mustela vison*) in southwest Britain. J. Zool. (London) 192: 205-223.

Cowan, I. M.; Wood, A. J.; Kitts, W. D. (1957) Feed requirements of deer, beaver, bear, and mink for growth and maintenance. Trans. North Am. Wildl. Conf. 22: 179-188.

Cowan, W. F.; Reilly, J. R. (1973) Summer and fall foods of mink on the J. Clark Salyer National Wildlife Refuge. Prairie Nat. 5: 20-24.

Eagle, T. C.; Whitman, J. S. (1987) Mink. In: Novak, M.; Baker, J. A.; Obbarel, M. E.; et al., eds. Wild furbearer management and conservation. Pittsburgh, PA: University of Pittsburgh Press; pp. 615-624.

Eberhardt, L. E. (1974) Food habits of prairie mink (*Mustela vison*) during the waterfowl breeding season [master's thesis]. St. Paul, MN: University of Minnesota.

Eisenberg, J. F. (1981) The mammalian radiations. Chicago, IL: University of Chicago Press.

Enders, R. K. (1952) Reproduction of the mink (*Mustela vison*). Proc. Am. Philos. Soc. 96: 691-755.

Errington, P. L. (1939) Reactions of muskrat populations to drought. Ecology 20: 168-186.

Errington, P. L. (1954) The special responsiveness of minks to epizootics in muskrat populations. Ecol. Monogr. 24: 377-393.

Ewer, R. F. (1973) The carnivores. Ithaca, NY: Cornell University Press.

Farrell, D. J.; Wood, A. J. (1968a) The nutrition of the female mink (*Mustela vison*). I. The metabolic rate of the mink. Can. J. Zool. 46: 41-46.

Farrell, D. J.; Wood, A. J. (1968b) The nutrition of the female mink (*Mustela vison*). II. The energy requirement for maintenance. Can. J. Zool. 46: 47-52.

Farrell, D. J.; Wood, A. J. (1968c) The nutrition of the female mink (*Mustela vison*). III. The water requirement for maintenance. Can. J. Zool. 46: 53-56.

Gerell, R. (1970) Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. Oikos 20: 451-460.

Gilbert, F. F.; Nancekivell, E. G. (1982) Food habits of mink (*Mustela vison*) and otter (*Lutra canadensis*) in northeastern Alberta. Can. J. Zool. 60: 1282-1288.

Guilday, J. E. (1949) Winter food of Pennsylvania mink. Pennsylvania Game News 20: 12-32.

Hall, E. R. (1981) The mammals of North America. 2nd ed. New York, NY: John Wiley and Sons.

Hall, E. R.; Kelson, K. R. (1959) The mammals of North America. 1st ed. New York, NY: The Ronald Press Co.

Hamilton, W. J., Jr. (1936) Food habits of the mink in New York. J. Mammal. 17: 169.

Hamilton, W. J., Jr. (1940) The summer food of minks and raccoons on the Montezuma Marsh, New York. J. Wildl. Manage. 4: 80-84.

Hamilton, W. J., Jr. (1959) Foods of mink in New York. N.Y. Fish and Game J. 6: 77-85.

Harding, A. R. (1934) Mink trapping. Columbus, OH: A. R. Harding.

Harper, R. H.; Travis, H. F.; Glinsky; M. S. (1978) Metabolizable energy requirement for maintenance and body composition of growing farm raised male mink (*Mustela vison*). J. Nutr. 108: 1937-1943.

Hornshaw, T. C.; Aulerich, R. J.; Johnson, H. E. (1983) Feeding Great Lakes fish to mink: effects on mink and accumulation and elimination of PCBs by mink. J. Toxicol. Environ. Health 11: 933-946.

Humphrey, S. R.; Zinn, T. L. (1982) Seasonal habitat use by river otters and everglades mink. J. Wildl. Manage. 46: 375-381.

Iversen, J. A. (1972) Basal energy metabolism of mustelids. J. Comp. Physiol. 81: 341-344.

Korschgen, L. J. (1958) December food habits of mink in Missouri. J. Mammal. 39: 521-527.

Kostron, K.; Kukla, F. (1970) Changes in thermoregulation in mink kits within the 45 days of ontogenesis. Acta Univ. Agric., Facultas Agronomica, Sbornik Vysoke Skoly Zemedelske (Brunn) (rada A) 18: 461-469.

Linn, I. J.; Birks, J. D. (1981) Observations on the home ranges of feral American mink (*Mustela vison*) in Devon, England, as revealed by radio-tracking. In: Chapman, J. A.; Pursley, D., eds. Proceedings worldwide furbearer conference: v. 1. August 1980; Frostburg, MD; pp. 1088-1102.

Linscombe, G.; Kinler, N.; Aulerich, R. J. (1982) Mink. In: Chapman, J. A.; Feldhammer, G. A., eds. Wild mammals of North America. Baltimore, MD: Johns Hopkins University Press; pp. 329-643.

Marshall, W. H. (1936) A study of the winter activities of the mink. J. Mammal. 17: 382-392.

McCabe, R. A. (1949) Notes on live-trapping mink. J. Mammal. 30: 416-423.

McDonnell, J. A.; Gilbert, F. F. (1981) The responses of muskrats (*Ondatra zibethicus*) to water level fluctuations at Luther Marsh, Ontario. In: Chapman, J. A.; Pursley, D., eds. Proceedings worldwide furbearer conference: v. 1. August 1980; Frostburg, MD; pp. 1027-1040.

Melquist, W. E.; Whitman, J. S.; Hornocker, M. G. (1981) Resource partitioning and coexistence of sympatric mink and river otter populations. In: Chapman, J. A.; Pursley, D., eds. Proceedings worldwide furbearer conference: v. 1. August 1980; Frostburg, MD; pp. 187-220.

Mitchell, J. L. (1961) Mink movements and populations on a Montana river. J. Wildl. Manage. 25: 48-54.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

National Research Council (NRC) (1982) Nutrient requirements of mink and foxes. In: Nutrient requirements of domestic animals series, No. 7. Washington, DC: National Academy of Sciences, National Academy Press.

Palmer, E. L.; Fowler, H. S. (1975) Fieldbook of natural history. New York, NY: McGraw-Hill Book Co.

Pendleton, G. W. (1982) A selected annotated bibliography of mink behavior and ecology. Brookings, SD: South Dakota State University; Tech. Bull. No. 3.

Perel'dik, N. S.; Milovanov, L. V.; Erin, A. T. (1972) Feeding fur bearing animals. Washington, DC: Translated from Russian by the Agricultural Research Service, U.S. Department of Agriculture and the National Science Foundation.

Proulx, G.; McDonnell, J. A.; Gilbert, F. F. (1987) The effect of water level fluctuations on muskrat, *Ondatra zibethicus*, predation by mink, *Mustela vison*. Can. Field-Nat. 101: 89-92.

Sargeant, A. B.; Swanson, G. A.; Doty, H. (1973) Selective predation by mink, *Mustela vison*, on waterfowl. Am. Midl. Nat. 89: 208-214.

Sealander, J. A. (1943) Winter food habits of mink in southern Michigan. J. Wildl. Manage. 7: 411-417.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Svilha, A. (1931) Habits of the Louisiana mink (*Mustela vison vulgivagus*). J. Mammal. 12: 366-368.

Williams, T. M. (1980) A comparison of running and swimming energetics in the mink (abstract). Am. Zool. 20: 909.

Williams, T. M. (1983) Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. J. Exp. Biol. 103: 155-168.

2.2.5. River Otter

<u>Order *Carnivora,* Family *Mustelidae*</u>. Mustelids have long, slender bodies, short legs, and anal scent glands. Throughout the family, the male is usually larger than the female. The more terrestrial species of this family occupy various habitats and feed primarily on small mammals and birds. Mustelids that live around lakes and streams feed primarily on aquatic species such as fish, frogs, and invertebrates (Palmer and Fowler, 1975; Burt and Grossenheider, 1980).

Selected species

The northern river otter (*Lutra canadensis*) historically lived in or near lakes, marshes, streams, and seashores throughout much of the North American continent (Hall, 1981). Currently, many populations along the coastal United States and Canada are stable or increasing, but this species is rare or extirpated throughout much of the midwestern United States (Toweill and Tabor, 1982). The river otter dens in banks and hollow logs. Individuals range over large areas daily, feeding primarily on fish. Although otters have few natural predators, while on land, they may be taken by coyotes, fox, or dogs (Melquist and Hornocker, 1983). Otters clean themselves frequently by rubbing and rolling in any dry surface (Toweill and Tabor, 1982). Otters appear to undergo bradycardia while submerged and can stay underwater for up to 4 minutes (Melquist and Dronkert, 1987). Because of its piscivorous diet and high trophic level, the river otter is a noteworthy indicator of bioaccumulative pollution in aquatic ecosystems (Melquist and Dronkert, 1987).

Body size. **River otters measure 66 to 76 cm with a 30 to 43 cm tail. Sexual dimorphism in size is seen among all subspecies (Harris, 1968; van Zyll de Jong, 1972, cited in Toweill and Tabor, 1982), and adult males (5 to 10 kg) outweigh females (4 to 7 kg) by approximately 17 percent (Melquist and Hornocker, 1983; see Table). Full adult weight generally is not attained until sexual maturity after 2 years of age (Melquist and Hornocker, 1983). Along the Pacific Coast, there is some evidence that size decreases from north to south (Toweill and Tabor, 1982).**

Metabolism. **Iversen (1972) found that basal metabolic rate of otters and other mustelids weighing 1 kg or more could be expressed by the equation:**

$$BMR = 84.6Wt^{0.78} (\pm 0.15),$$

where BMR = basal metabolic rate in kcal/day and Wt = body weight in kilograms. Free-living metabolic rates would be expected to be three to five times higher (see table).

Habitat. **Almost exclusively aquatic, the river otter is found in freshwater, estuarine, and some marine environments all the way from coastal areas to mountain lakes (Toweill and Tabor, 1982). They are found primarily in food-rich coastal areas, such as the lower portions of streams and rivers, estuaries, nonpolluted waterways, the lakes and tributaries that feed rivers, and areas showing little human impact (Mowbray et al., 1979; Tabor and Wight, 1977).**

Food habits. **Otters usually are active in the evening and from dawn to midmorning, although they can be active any time of day (Melquist and Hornocker, 1983). The bulk of the river otter's diet is fish; however, otters are opportunistic and will feed on a variety of prey depending on availability and ease of capture. River otters take different fish species according to their availability and how well the fish can escape capture (Loranger, 1981). Depending on availability, otters also may consume crustaceans (especially crayfish), aquatic insects (e.g., stonefly nymphs, aquatic beetles), amphibians, insects, birds (e.g., ducks), mammals (e.g., young beavers), and turtles (Burt and Grossenheider, 1980; Lagler and Ostenson, 1942; Liers, 1951b; Melquist and Hornocker, 1983; Palmer and Fowler, 1975; Toweill and Tabor, 1982). Gilbert and Nancekivell (1982) observed that otters consume more waterfowl in the northerly latitudes than in the south, probably because of the ease of capturing the waterfowl during their molt in the north. Otters probe the bottoms of ponds or streams for invertebrates and may ingest mud or other debris in the process (Liers, 1951b). Otters in captivity required 700-900 g of food daily (Harris, 1968, cited in Toweill and Tabor, 1982).**

Temperature regulation and molt. **Seasonal patterns in otters are not well understood. Otters are active throughout the year (Toweill and Tabor, 1982), with the most intense activity levels during the winter (Larsen, 1983; Melquist and Hornocker, 1983). They undergo a gradual molt in spring and fall (Melquist and Dronkert, 1987).**

***Breeding activities and social organization*. Adult males are usually solitary; an adult female and two or three pups make up a typical family group (Melquist and Dronkert, 1987). River otters breed in late winter or early spring over a period of 3 months or more. Birth of a litter follows mating by about 1 year; however, implantation is delayed for approximately 10 months, and active gestation lasts only 2 months (Pearson and Enders, 1944, cited in Toweill and Tabor, 1982; Melquist and Dronkert, 1987). Newborn otters are born blind but fully furred and depend on their mother for milk until 3 to 5 months of age (Johnstone, 1978; Liers, 1951b). Family groups disperse about 3 months after the pups are weaned (Melquist and Hornocker, 1983).**

Home range and resources. **The river otter's home range encompasses the area needed for foraging and reproduction (Melquist and Dronkert, 1987). The shape of the home range varies by habitat type; for example, near rivers or coastal areas, it may be a long strip along the shoreline (measured in kilometers), but in marshes or areas with many small streams, the home range may resemble a polygon (measured in hectares; Melquist and Dronkert, 1987). All parts of a home range are not used equally; instead, several activity centers may be interconnected by a stream or coast (Melquist and Hornocker, 1983). Food has the greatest influence on habitat use, but adequate shelter in the form of temporary dens and resting sites also plays a role (Anderson and Woolf, 1987a; Melquist and Hornocker, 1983). River otters use dens dug by other animals or natural shelters such as hollow logs, logjams, or drift piles (Toweill and Tabor, 1982; Melquist and Dronkert, 1987). Beaver bank dens and lodges accounted for 38 percent of resting sites used by radio-tracked otters in Idaho (Melquist and Hornocker, 1983). River otters appear to prefer flowing water habitats (e.g., streams) over more stationary water (e.g., lakes, ponds) (Idaho study; Melquist and Hornocker, 1983).**

River otters maintain distinct territories within their home ranges: females maintain a feeding area for their families, males for breeding purposes (Toweill and Tabor, 1982). Individuals tend to avoid confrontation through mutual avoidance (Melquist and Hornocker, 1983). Home ranges are most restricted for lactating females (Melquist and Dronkert, 1987). Adult and subadult males have larger, more variable home ranges than females.

Population density. **River otter populations show variable spacing in relation to prey density and habitat (Hornocker et al., 1983). This characteristic, along with their secretive habits and use of several den sites, makes it difficult to estimate river otter populations (Melquist and Dronkert, 1987). Population density of otters often is expressed in terms of number per kilometer of waterway or coastline because of their dependence on aquatic habitats. Densities between one otter every kilometer to one otter every 10 km of river or shoreline are typical (see table).**

Population parameters. **Otters generally are not sexually mature until 2 years of age (Liers, 1951b; Hamilton and Eadie, 1964; Tabor and Wight, 1977; Lauhachinda, 1978). Adult females appear to reproduce yearly in Oregon (based on a pregnancy rate of almost 100 percent; Tabor and Wight, 1977), but Lauhachinda (1978) concluded that they breed every other year in Alabama and Georgia. Litters usually consist of two to three pups, although litters as large as six pups occur (see table). As adults, river otter mortality rates are low, between 15 and 30 percent per year (Lauhachinda, 1978; Tabor and Wight, 1977).**

Similar species (from general references)

- **The sea otter (*Enhydra lutris*) (76 to 91 cm body and 28 to 33 cm tail; weight 13 to 38 kg) inhabits kelp beds and rocky shores from the Aleutian Islands to California. Its diet includes fish, abalones, sea urchins, and other marine animals.**

General references

Burt and Grossenheider (1980); Melquist and Dronkert (1987); Palmer and Fowler (1975); Toweill and Tabor (1982).

River Otter (*Lutra canadensis*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Weight (kg)	A B		5.0 - 15	throughout range	Melquist & Dronkert, 1987	1
	A M A F Y M Y F	8.13 ± 1.15 SD 6.73 ± 1.00 SD 6.36 ± 0.98 SD 5.83 ± 1.82 SD	5.84 - 10.4 4.74 - 8.72 4.41 - 8.31 3.75 - 7.01	Alabama, Georgia	Lauhachinda, 1978	
	A M A F Y M Y F	9.20 ± 0.6 SE 7.90 ± 0.2 SE 7.90 ± 0.4 SE 7.20 ± 0.1 SE		wc Idaho	Melquist & Hornocker, 1983	
	neonate neonate	0.132 0.140 to 0.145		New York Alabama, Georgia	Hamilton & Eadie, 1964 Hill & Lauhachinda, 1981	
Pup Growth Rate (g/day)	10 to 20 days	26.7		NS	Liers, 1951a	2
Metabolic Rate (kcal/kg-day)	A F basal A M basal	44.8 42.6			estimated	3
	A F free-living A M free-living	183 178	(83 - 400) (81 - 391)		estimated	4
Food Ingestion Rate (g/g-day)						5
Water Ingestion Rate (g/g-day)	A F A M	0.082 0.080			estimated	6
Inhalation Rate (m^3/day)	A F A M	2.5 2.9			estimated	7
Surface Area (cm^2)	A F A M	3,785 4,280			estimated	8

River Otter (*Lutra canadensis*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
fish	100	93	97	99	wc Idaho/mountain streams and lakes	Melquist & Hornocker, 1983	
(sucker)	(52)	(47)	(17)	(30)			
(sculpins)	(40)	(31)	(38)	(42)	(percent frequency of occurrence in scats)		
(squawfish)	(5)	(4)	(1)	(6)			
(perch)	(22)	(3)	(7)	(9)			
(whitefish)	(21)	(10)	(24)	(66)			
invertebrates	2	7	10	12	(most of the fish were longer than 30 cm)		
birds	<1	12	1	<1			
mammals	1	4	3	1			
reptiles	0	1	0	0			
invertebrates	41.6	44.2	33.3	26.3	nw Montana/ lakes and streams	Greer, 1955	
(aquatic insects)	19.6	19.2	10.7	4.0			
(fr water shrimp)	14.3	8.9	10.7	4.0			
fishes	91.4	92.9	100	100	(percent frequency of occurrence in scats)		
(trout)	23.7	9.8	33.3	29.3			
(sculpin)	20.5	20.9	21.3	25.3			
(sunfish)	47.1	72.8	60.0	33.3			
frog	19.6	19.2	10.7	9.1			
salamander	0.3	0.7	1.3	--			
snake	0.2	0.7	--	--			
birds	6.7	4.1	1.3	1			
mammals	8.1	5.3	2.7	4.0			
fish	97	69	98	99	nw Illinois/Mississippi River	Anderson & Woolf, 1987b	
(sunfish)	(31)	(31)	(80)	(52)			
(minnow/carp)	(52)	(0)	(17)	(44)	(percent frequency of occurrence in scats)		
(herring)	(49)	(38)	(10)	(40)			
(bass)	(26)	(0)	(5)	(14)			
frogs	3	6	11	16			
crayfish	12	50	8	7			
dragonfly nymphs	2	0	6	2			
birds	4	13	3	1			

River Otter (*Lutra canadensis*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
game & pan fish forage fish fish remains amphibians other invertebrates	32 17.6 3.0 16.1 25.8				Michigan/habitat NS (% volume; stomach contents)	Lagler & Ostenson, 1942	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha or km river)	A B		400 - 1,900 ha	Missouri/marsh, streams	Erickson et al., 1984	9
	A B		2,900 - 5,700 ha	Colorado (fall-spr)/NS	Mack, 1985	9
	A M A F	400 ha 295 ha		se Texas/coastal marsh	Foy, 1984	9
	yearling M yearling F adult F B B	43 ± 20 SD km 32 ± 6.2 SD km 31 ± 9.2 SD km 28 ± 7.5 SD km	10 - 78 km 25 - 40 km 23 - 50 km 15 - 39 km	wc Idaho/river drainage (no trends seen with season)	Melquist & Hornocker, 1983	
Population Density (N/ha or N/km shoreline)	B B A F breeding A M breeding yearling B	0.26/km 0.05/km 0.019/km 0.071/km	0.17 - 0.37/km	wc Idaho/river drainage	Melquist & Hornocker, 1983	
	B B	0.85/km		se Alaska/coastal - island	Woolington, 1984	9
	B B		0.0094 - 0.014 /ha	se Texas/coastal marsh	Foy, 1984	9
	A B	0.0025/ha		Missouri/marsh, streams	Erickson et al., 1984	9

River Otter (*Lutra canadensis*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Litter Size		2.73 ± 0.77 SD	1 - 4	Maryland/wetlands	Mowbray et al., 1979	10
		2.68 ± 0.71 SD	1 - 4	Alabama, Georgia/NS	Hill & Lauhachinda, 1981	
		2.1 ± 0.7 SD		New York/NS	Hamilton & Eadie, 1964	
	1 yr old	0.53 ± 0.91 SD	0 - 3	Maine/NS	Docktor et al., 1987	11
	2 yr old	0.87 ± 0.96 SD	0 - 3			
	3 yr old	1.60 ± 1.42 SD	0 - 4			
	4 yr old	2.29 ± 1.25 SD	1 - 5			
	5 to 12 yrs old	2.67 ± 1.40 SD	0 - 6			
Litters /Year		1		NS	Trippensee, 1953	
Days Gestation	total		290 - 380	Wisconsin/captive	Liers, 1951b	12
	active	60-63		NS	Lancia & Hair, 1983	13
Age at Weaning			> 90 days	NS	Harris, 1968	
Age at Sexual Maturity	F	2 yrs		New York/NS	Hamilton & Eadie, 1964	
	M	2 yrs				
Annual Mortality Rates (percent)	birth - 1 yr	32		Oregon/NS	Tabor & Wight, 1977	
	1 - 2 yrs	54				
	2 - 11 yrs	27				
	A M	17.8		Alabama, Georgia/riverine	Lauhachinda, 1978	
	A F	20.3				
Longevity	A B		< 15 yrs	Alabama, Georgia/riverine	Lauhachinda, 1978	

River Otter (*Lutra canadensis*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	January March winter	March to April late winter	May April spring	Michigan New York AL, FL, GA	Hooper & Ostenson, 1949 Hamilton & Eadie, 1964 Lauhachinda, 1978	14
Parturition	mid-March late March late January		mid-May early April May	Maryland, Chesapeake Bay wc Idaho Alabama	Mowbray et al., 1979 Melquist & Hornocker, 1983 Lauhachinda, 1978	
Dispersal		April to May		wc Idaho	Melquist & Hornocker, 1983	15

1 Summary of studies discussed by Hall (1981) and Woolington (1984).
2 Cited in Toweill and Tabor (1982).
3 Estimated using equation 3-43 (Boddington, 1978) and adult body weights from Lauhachinda (1978).
4 Estimated using equation 3-47 (Nagy, 1987) and adult body weights from Lauhachinda (1978).
5 See Chapters 3 and 4 for methods of estimating food ingestion rates.
6 Estimated using equation 3-17 (Calder and Braun, 1983) and adult body weights from Lauhachinda (1978).
7 Estimated using equation 3-20 (Stahl, 1967) and adult body weights from Lauhachinda (1978).
8 Estimated using equation 3-22 (Stahl, 1967) and adult body weights from Lauhachinda (1978).
9 Cited in Melquist and Dronkert (1987).
10 Determined from implanted embryo counts.
11 Determined from corpora lutea counts.
12 Total gestation period (including preimplantation).
13 Active gestation period (postimplantation), cited in Melquist and Dronkert (1987).
14 Cited in Toweill and Tabor (1982).
15 Dispersal at age 12 to 13 months.

References (including Appendix)

Alexander, G. (1977) Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10: 181-195.

Anderson, K. L. (1981) Population and reproduction characteristics of the river otter in Virginia and tissue concentrations of environmental contaminants [master's thesis]. Blacksburg, VA: Virginia Polytechnic Institute.

Anderson, K. L.; Scanlon, P. F. (1981) Reproduction and population characteristics of river otters in Virginia. Virginia J. Sci. 32: 87.

Anderson, E. A.; Woolf, A. (1987a) River otter habitat use in northwestern Illinois. Trans. Illinois Acad. Sci. 80: 107-114.

Anderson, E. A.; Woolf, A. (1987b) River otter food habits in northwestern Illinois. Trans. Illinois Acad. Sci. 80: 115-118.

Boddington, M. J. (1978) An absolute metabolic scope for activity. J. Theor. Biol. 75: 443-449.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Chabreck, R. H.; Holcombe, J. E.; Linscombe, R. G.; et al. (1982) Winter foods of river otters from saline and fresh environments in Louisiana. Proc. Annu. Conf. Southeast Assoc. Fish Wildl. Agencies 36: 473-483.

Docktor, C. M.; Bowyer, T. R.; Clark, A. G. (1987) Number of corpora lutea as related to age and distribution of river otter in Maine. J. Mammal. 68: 182-185.

Eisenberg, J. F. (1981) The mammalian radiations; an analysis of trends in evolution, adaptation, and behavior. Chicago, IL: University of Chicago Press.

Erickson, D. W.; McCullough, C. R.; Porath, W. R. (1984) River otter investigations in Missouri. Missouri Dept. Conserv.; Pittman-Robertson Proj. W-13-R-38, Final Report.

Foy, M. K. (1984) Seasonal movement, home range, and habitat use of river otter in southeastern Texas [master's thesis]. College Station, TX: Texas A&M University.

Gilbert , F. F.; Nancekivell, E. G. (1982) Food habits of mink (*Mustela vison*) and otter (*Lutra canadensis*) in northeastern Alberta. Can. J. Zool. 60: 1282-1288.

Greer, K. R. (1955) Yearly food habits of the river otter in the Thompson Lakes region, Northwestern Montana, as indicated by scat analyses. Am. Midl. Nat. 54: 299-313.

Greer, K. R. (1956) Fur resources and investigations: study of the otter food habits along a segment of the Gallatin River. Montana Fish and Game Dept.; Job Comp. Rep. W-049-R-06:35-59.

Grenfell, W. E., Jr. (1974) Food habits of the river otter in Suisin Marsh, central California [master's thesis]. Sacramento, CA: California State University.

Grinnell, J.; Dixon, J. S.; Linsdale, J. M. (1937) Fur-bearing mammals of California. Berkeley, CA: University of California Press.

Hall, E. R. (1981) The mammals of North America. 2nd ed. New York, NY: John Wiley and Sons.

Hall, E. R.; Kelson, K. R. (1959) The mammals of North America. 1st ed. New York, NY: The Ronald Press Co.

Hamilton, W. J., Jr. (1961) Late fall, winter and early spring foods of 141 otters from New York. N. Y. Fish and Game J. 8: 106-109.

Hamilton, W. J., Jr.; Eadie, W. R. (1964) Reproduction in the otter, *Lutra canadensis*. J. Mammal. 45: 242-252.

Harris, C. J. (1968) Otters: a study of the recent Lutrinae. London, U.K.: Weidenfield & Nicolson.

Harris, J. (1969) Breeding the Canadian otter *Lutra c. canadensis* in a private collection. Int. Zoo Yearbook 9: 90-91.

Hill, E. P.; Lauhachinda, V. (1981) Reproduction in river otters from Alabama and Georgia. In: Chapman, J. A.; Pursley, D., eds. Proceedings worldwide furbearer conference: v. 1. August 1980; Frostburg, MD.

Hooper, E. T.; Ostenson, B. T. (1949) Age groups in Michigan otter. Ann Arbor, MI: University of Michigan; Mus. Zool. Occas. Pap. 518.

Hornocker, M. G.; Messick, J. P.; Melquist, W. E. (1983) Spacial strategies in three species of Mustelidae. Acta Zool. Fenn. 174: 185-188.

Humphrey, S. R.; Zinn, T. L. (1982) Seasonal habitat use by river otters and Everglades mink. J. Wildl. Manage. 46: 375-381.

Iversen, J. A. (1972) Basal energy metabolism of Mustelids. J. Comp. Physiol. 81: 341-344.

Johnstone, P. (1978) Breeding and rearing the Canadian otter (*Lutra canadensis*) at Mole Hall Wildlife Park, 1966-1977. Int. Zoo Yearbook 18: 143-147.

Knudsen, G. J.; Hale, J. B. (1968) Food habits of otters in the Great Lakes region. J. Wildl. Manage. 32: 89-93.

Lagler, K. F.; Ostenson, B. T. (1942) Early spring food of the otter in Michigan. J. Wildl. Manage. 6: 244-254.

Lancia, R. A.; Hair, J. D. (1983) Population status of bobcat (*Felis rufus*) and river otter (*Lutra canadensis*) in North Carolina. Raleigh, NC: North Carolina State Univ., Proj. E-1; 65 pp.

Larsen, D. N. (1983) Habitats, movements, and foods of river otters in coastal southeastern Alaska [master's thesis]. Fairbanks, AL: University of Alaska.

Larsen, D. (1984) Feeding habits of river otters in coastal southeastern Alaska. J. Wildl. Manage. 48: 1446-1452.

Lauhachinda, V. (1978) Life history of the river otter in Alabama with emphasis on food habits [Ph.D. dissertation]. Auburn, AL: University of Alabama.

Liers, E. E. (1951a) My friends the land otters. Nat. Hist. 60: 320-326.

Liers, E. E. (1951b) Notes on the river otter (*Lutra canadensis*). J. Mammal. 32: 1-9.

Liers, E. E. (1966) Notes on breeding the Canadian otter *Lutra canadensis* in captivity and longevity records of beavers *Castor canadensis*. Int. Zoo Yearbook 6: 171-172.

Loranger, A. J. (1981) Late fall and early winter foods of the river otter (*Lutra canadensis*) in Massachusetts, 1976 - 1978. In: Chapman, J. A.; Pursley, D., eds. Worldwide furbearer conference proceedings, v 1; August 3-11, 1980; Frostburg, MD; pp. 599-605.

MacFarlane, R. (1905) Notes on mammals collected and observed in the northern Mackenzie River District. Proc. U.S. Natl. Mus. 23: 716-717.

Mack, C. M. (1985) River otter restoration in Grand County, Colorado [master's thesis]. Fort Collins, CO: Colorado State University.

McDaniel, J. C. (1963) Otter population study. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 17: 163-168.

Melquist, W. E.; Dronkert, A. E. (1987) River otter. In: Novak, M.; Baker, J. A.; Obbarel, M. E.; et al., eds. Wild furbearer management and conservation. Pittsburgh, PA: University of Pittsburgh Press; pp. 627-641.

Melquist, W. E.; Hornocker, M. G. (1983) Ecology of river otters in west central Idaho. In: Kirkpatrick, R. L., ed. Wildlife monographs: v. 83. Bethesda, MD: The Wildlife Society; 60 pp.

Melquist, W. E.; Whitman, J. S.; Hornocker, M. G. (1981) Resource partitioning and coexistence of sympatric mink and river otter populations. In: Chapman, J. A.; Pursley, D., eds. Worldwide furbearer conference proceedings, v 1; August 3-11, 1980; Frostburg, MD; pp. 187-220.

Modafferi, R.; Yocom, C. F. (1980) Summer food of river otter in north coastal California lakes. Murrelet 61: 38-41.

Mowbray, E. E.; Pursley, D.; Chapman, J. A. (1979) The status, population characteristics and harvest of the river otter in Maryland. Waverly Press; Maryland Wildl. Admin., Publ. Wildl. Ecol. 2; 16 pp.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Mono. 57: 111-128.

Palmer, E. L.; Fowler, H. S. (1975) Fieldbook of natural history. New York, NY: McGraw-Hill Book Co.

Pearson, O. P.; Enders, R. K. (1944) Duration of pregnancy in certain Mustelids. J. Exp. Zool. 95: 21-35.

Pierce, R. M. (1979) Seasonal feeding habits of the river otter (*Lutra canadensis*) in ditches of the Great Dismal Swamp [master's thesis]. Norfolk, VA: Old Dominion University.

Reid, D. G. (1984) Ecological interactions of river otters and beavers in a boreal ecosystem [master's thesis]. Calgary, Canada: University of Calgary.

Ryder, R. A. (1955) Fish predation by the otter in Michigan. J. Wildl. Manage. 19: 497-498.

Scheffer, V. B. (1958) Long life of a river otter. J. Mammal. 39: 591.

Sheldon, W. G.; Toll, W. G. (1964) Feeding habits of the river otter in a reservoir in central Massachusetts. J. Mammal. 45: 449-455.

Shirley, M. G. (1985) Spring food habits of river otter in southwestern Louisiana (abstract only). Proc. La. Acad. Sci. 48: 138.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Stenson, G. B.; Badgero, G. A.; Fisher, H. D. (1984) Food habits of the river otter *Lutra canadensis* in the marine environment of British Columbia. Can. J. Zool. 62: 88-91.

Tabor, J. E.; Wight, H. M. (1977) Population status of river otter in western Oregon. J. Wildl. Manage. 41: 692-699.

Toll, W. G. (1961) The ecology of the river otter (*Lutra canadensis*) in the Quabbin Reservation of central Massachusetts [master's thesis]. Amherst, MA: University of Massachusetts.

Toweill, D. E. (1974) Winter food habits of river otters in western Oregon. J. Wildl. Manage. 38: 107-111.

Toweill, D. E.; Tabor, J. E. (1982) River otter. In: Chapman, J. A.; Feldhammer, G. A., eds. Wild mammals of North America. Baltimore, MD: Johns Hopkins University Press; pp. 688-703.

Trippensee, R. E. (1953) Wildlife management: fur bearers, waterfowl, and fish. New York, NY: McGraw-Hill.

Tumlison, R.; Shalaway, S. (1985) An annotated bibliography on the North American river otter *Lutra canadensis*. Stillwater, OK: Okla. Fish Wildl. Res. Unit & Dept. Zool., Oklahoma State University.

van Zyll de Jong, C. G. (1972) A systematic review of the nearctic and neotropical river otters (Genus *Lutra*, Mustelidae, Carnivora). Ontario, Canada: R. Ontario Mus., Life Sci. Contr. 80.

Wilson, K. A. (1959) The otter in North Carolina. Proc. Southeast. Assoc. Fish and Game Comm. 13: 267-277.

Wilson, K. A. (1985) The role of mink and otter as muskrat predators in northeastern North Carolina. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 18: 199-207.

Woolington, J. D. (1984) Habitat use and movements of river otters at Kelp Bay, Baranof Island, Alaska [master's thesis]. Fairbanks, AK: University of Alaska.

2.2.6. Harbor Seal (hair seals)

<u>Order *Carnivora*, Family *Phocidae*</u>. Seals, sea lions, and walruses are collectively referred to as pinnipeds (Latin for wing-footed). Pinnipeds are divided into three families: otarids (sea lions and fur seals); phocids (hair seals, also called true seals or earless seals); and walruses. Most pinnipeds feed on marine species such as fish, squid, and other invertebrates (Burt and Grossenheider, 1980). Unlike fur seals, which are protected from the cold marine environment by a dense layer of underfur, phocids rely only on a thick blubber layer for insulation (Pierotti and Pierotti, 1980). Phocids include both the smallest (ring seals) and the largest (elephant seals) of the pinnipeds. The geographic range of most phocid species is from the arctic Atlantic and Pacific south to the coasts of Canada and Alaska, although some do inhabit warmer water (Burt and Grossenheider, 1980). Most phocids, with the exception of the elephant seal, do not exhibit the large disparity in size between the sexes, which is characteristic of otarids (sea lions and fur seals) (Burt and Grossenheider, 1980).

Selected species

In North America, harbor seals (*Phoca vitulina*) range from Alaska to Baja California, Mexico, along the Pacific coast (subspecies *richardsi*; Hoover, 1988), and from Newfoundland to eastern Long Island along the Atlantic coast (subspecies *concolor*; Payne and Selzer, 1989). They are one of the most commonly seen pinniped species, in part due to their tendency to inhabit coastal areas (Hoover, 1988). Harbor seals can be found along the Pacific coast on a year-round basis (except during stormy periods in winter), but Atlantic populations winter offshore when coastal ice has formed in their usual haul-out areas (Boulva and McLaren, 1979). The recent increases in harbor seal populations in New England waters appear to be due to a southward dispersal of seals from rookeries in Maine following the termination of a Massachusetts bounty on harbor seals (1962) and the passage of the Marine Mammal Protection Act (1972) (Payne and Schneider, 1984).

The spotted or largha seal (*Phoca largha*) is a closely related species that until recently was considered a subspecies of the harbor seal. It is similar in size, appearance, and feeding habits to the Pacific harbor seal, but it tends to inhabit colder waters along the Pacific coasts (Ashwell-Erickson and Elsner, 1981). In North America, it seldom ventures further south than the northern coast of Alaska (Ashwell-Erickson and Elsner, 1981). The spotted seal requires ice for breeding haul-outs and gives birth about 2 months earlier than the Pacific harbor seal (Ashwell-Erickson and Elsner, 1981; Boulva and McLaren, 1979). The harbor seal, in contrast, breeds on land (Boulva and McLaren, 1979).

***Body size*. The length and weight of harbor seals vary geographically, but sexually mature adults tend to be about 1.5 m in length and weigh from 65 to 90 kg (Ashwell-Erickson and Elsner, 1981; Pitcher and Calkins, 1979). Harbor seals exhibit some sexual dimorphism, the male being larger (Pitcher and Calkins, 1979). Body length usually is used to measure size because weight can vary substantially with factors such as season, food availability, and molting (Ronald et al., 1982). Newborn pups are around 80 cm long and weigh from 8.6 to almost 15 kg, with females often weighing less than males (Newby, 1973; Pitcher and Calkins, 1979; Rosen, 1989). Harbor seal pups are highly precocial and are**

able to swim within hours of birth (Boulva and McLaren, 1979; Lawson and Renouf, 1987). Seal milk consists of about half fat, and the pups more than double their weight before they are weaned at approximately 30 days (Bigg, 1969a, as cited in Pitcher and Calkins, 1979). Harbor seals continue to grow with age for several years beyond the age of sexual maturity (Boulva and McLaren, 1979; Pitcher and Calkins, 1979). Body fat varies seasonally with food intake, while total body weight and lean body mass increase with age (Ashwell-Erickson and Elsner, 1981). Harbor seals, unlike many other pinnipeds, do not fast for extended periods during the molting period or breeding season (Boulva and McLaren, 1979; Pierotti and Pierotti, 1980).

***Habitat*.** Harbor seals inhabit a variety of environments and are able to tolerate a wide range of temperatures and water salinities (Boulva and McLaren, 1979; Hoover, 1988). In its eastern range, the harbor seal inhabits inlets, islets, reefs, and sandbars (Boulva and McLaren, 1979). In western North America, the harbor seal inhabits tidal mud flats, sand bars, shoals, river deltas, estuaries, bays, coastal rocks, and offshore islets (Johnson and Jeffries, 1977), even ranging up rivers into freshwater areas in search of food (Roffe and Mate, 1984). Harbor seals also inhabit some freshwater lakes (Power and Gregoire, 1978). Habitats used for haul-outs include cobble and sand beaches, tidal mud flats, offshore rocks and reefs, glacial and sea ice, and man-made objects such as piers and log booms (Hoover, 1988).

***Food habits*.** Harbor seals' diet varies seasonally and includes bottom-dwelling fishes (e.g., flounder, sole, eelpout), invertebrates (e.g., octopus), and species that can be caught in periodic spawning aggregations (e.g., herring, lance, squid) (Everitt et al., 1981; Lowry and Frost, 1981; Pitcher and Calkins, 1979; Roffe and Mate, 1984).[g] Harbor seals are opportunistic, consuming different prey in relation to their availability and ease of capture (Pitcher and Calkins, 1979; Pitcher, 1980; Shaffer, 1989). They may move into rivers on a seasonal basis in pursuit of prey (e.g., eulachon in the Columbia River during winter; Brown et al., 1989). They hunt alone or in small groups (Hoover, 1988). Fish species consumed range between 40 and 280 mm, with mean values of between 60 and 180 mm (Brown and Mate, 1983). Recently weaned pups tend to feed on prey that are more easily captured than fish, such as shrimp or other crustaceans (Hoover, 1988; Pitcher and Calkins, 1979). During the breeding and molting seasons, when harbor seals spend more time on land, adults rely on their blubber layer as an additional source of energy (Ashwell-Erickson and Elsner, 1981). During this time, they may be more susceptible to lipophilic contaminants (e.g., PCBs) that may have accumulated in their blubber (Hoover, 1988).

---

[g] Studies of harbor seal diet often rely on counts of fish sagittal otoliths found in scats or stomach contents. These otoliths can be identified to the level of species, annuli on the otoliths counted to determine age, and fish weights and lengths estimated from otolith dimensions. However, partial or complete digestion of otoliths, particularly of small fish species, may result in significant underestimates of the proportion of these prey in seal diets, particularly from scat analysis (da Silva and Neilson, 1985; Harvey, 1989). Studies of stomach contents of stranded seals also may present a biased picture of dietary composition due to extended periods of fasting prior to stranding (Selzer et al., 1986).

In general, food consumption by adult seals is highest in winter and lowest in the summer (Ashwell-Erickson and Elsner, 1981; Ashwell-Erickson et al., 1979). Innes et al. (1987) estimated allometric equations for maintenance food ingestion rates (IR; wet-weight biomass) with body weight (BW, kg) for phocids:

$IR_{maint}(kg/day) = 0.079\ BW(kg)^{0.71}$ **adult (N = 11; r^2 = 0.84);**

$IR_{maint}(kg/day) = 0.032\ BW(kg)^{1.00}$ **juveniles (N = 19; r^2 = 0.68); and**

$IR_{maint}(kg/day) = 0.068\ BW(kg)^{0.78}$ **both adults and juveniles (N = 30; r^2 = 0.68).**

Allometric equations for food ingestion rates of growing animals (IR; wet-weight biomass) with body weight (BW, kg) for phocids also have been estimated (Innes et al., 1987):

$IR_{growth}(kg/day) = 0.0919\ BW(kg)^{0.84}$ **adult (N = 11; r^2 = 0.84); and**

$IR_{growth}(kg/day) = 0.0547\ BW(kg)^{0.84}$ **juveniles (N = 19; r^2 = 0.68).**

Innes et al. (1987) found that growing juvenile phocid seals ingested 1.7 times more biomass per day than a similar-sized growing adult and 1.4 times more than juvenile phocids that were not growing.

Boulva and McLaren (1979) estimated a relationship between body weight and daily food ingestion for harbor seals from eastern Canada:

$IR_{free\text{-}living}(kg/day) = 0.089\ BW(kg)^{0.76}$ **adults (N = 26).**

Perez (1990) estimated the average energy value of the harbor seal's diet to be 1.4 kcal/g wet weight. Ashwell-Erickson and Elsner (1981) provide age-specific estimates of food ingestion rates for the closely related spotted seal (see Appendix) and summarize studies in which food ingestion rates for harbor and spotted seals have been estimated.

Temperature regulation and molt. **Harbor seals can maintain their heat balance while diving in water as low as 13°C without increased muscle activity or metabolic rate (Ronald et al., 1982). For seals in general, molting is simply part of an ongoing pelage cycle that is influenced by the seal's environment, physiology, and behavior (Ling, 1974). Phocids get an entirely new coat with each annual molt (Ling, 1970), a process that takes about 5 weeks (Scheffer and Slipp, 1944, as cited in Ashwell-Erickson and Elsner, 1981). During their molt, they spend more time hauled and exhibit a slower metabolic rate (e.g., 83 percent of premolt levels), which decreases their food requirements (Ashwell-Erickson and Elsner, 1981). After molting, harbor seals increase their fat reserves (and weight) for the winter and early spring; metabolic rates also might be lowered during this time to conserve energy (Renouf, 1989).**

Breeding activities and social organization**. The timing of reproduction in harbor seals varies with location. Mating and pupping are initiated earlier in the year in more**

southern latitudes, but within populations, breeding is synchronized (Hoover, 1988; Slater and Markowitz, 1983). Harbor seals may form large breeding aggregations on land in areas where food resources are plentiful (Slater and Markowitz, 1983); however, pupping activities are not restricted to large, discrete rookeries (Pitcher and Calkins, 1979). Mating occurs soon after weaning, which is 3 to 6 weeks after birth (Ashwell-Erickson and Elsner, 1981). It is likely that harbor seals are promiscuous (Pierotti and Pierotti, 1980), although there is some evidence that they are mildly polygynous, with males defending territories at the haul-out sites (Boulva and McLaren, 1979; Perry, 1989; Slater and Markowitz, 1983). Following mating, implantation is delayed for 1.5 to 3 months, during which time the female molts (Bigg, 1969a; Hoover, 1988; Pitcher and Calkins, 1979). At other times of the year, harbor seals also can be found in groups of 30 to 80 in some haul-out areas (Hoover, 1988).

***Home range and resources*. Harbor seals generally inhabit highly productive coastal areas, with upwelling ocean currents that bring nutrients to the surface supporting abundant marine life (e.g., the California current system, the Gulf of Alaska, and the Gulf of Maine; Ronald et al., 1982). Harbor seals also require adequate places to haul out, and their distribution is influenced by the availability of suitable sites (Boulva and McLaren, 1979). In general, seals stay near particular haul-out sites with only local movements (Brown and Mate, 1983; Pitcher and Calkins, 1979; Slater and Markowitz, 1983). Haul-out patterns are determined by several factors, including weather, tidal pattern, time of day, season, and human proximity (Slater and Markowitz, 1983). Harbor seals are considered fairly sedentary, with individuals showing year-round site fidelity, although some seasonal movement associated with pupping and long-distance movements are recorded (Pitcher and Calkins, 1979; Slater and Markowitz, 1983). Data on likely daily or monthly foraging distances are lacking.**

***Population density*. Harbor seals are found principally in coastal areas within 20 km of shore; they tend to concentrate in estuaries and protected waters (Hoover, 1988). Their distribution is highly patchy, and local population densities in haul-out areas with favorable food resources nearby can be quite high (Pitcher and Calkins, 1979).**

***Population dynamics*. Females are sexually mature by 3 to 5 years of age, whereas males are sexually mature later, at 4 to 6 years of age (Boulva and McLaren, 1979; Pitcher and Calkins, 1979). Females only produce one pup per year (Hoover, 1988). Three major causes of preweaning pup mortality are stillbirth, desertion by the mother, and shark kills (Boulva and McLaren, 1979). Mortality from birth to 4 years of age was estimated to be 74 percent for females and 79 percent for males in one study, after which it remained at about 10 percent per year (Pitcher and Calkins, 1979). Life expectancy for harbor seals is about 30 years (Newby, 1978).**

Similar species (from general references)

- **The ringed seal (*Phoca hispida*) is smaller (1.4 m length; weight to 90 kg) than the harbor seal and inhabits colder waters. It feeds mainly on marine invertebrates.**

- **The harp seal (*Phoca groenlandicus*) (1.8 m; weight to 180 kg) inhabits deep, icy water. It ranges from the Arctic Atlantic south to Hudson Bay; it is only rarely found further south. It feeds on macroplankton and fish.**

- **The largha or spotted seal (*Phoca largha*) (1.5 m) is a closely related species that until recently was considered a subspecies of the harbor seal. Its characteristics are compared with those of the harbor seal under *Selected species.***

- **The ribbon seal (*Phoca fasciata*) (1.6 m; males to 90 kg, females to 76 kg) lives near pack ice in the Bering Sea and feeds on bottom invertebrates, fish, and octopus and squid.**

General references

Ashwell-Erickson and Elsner (1981); Burt and Grossenheider (1980); Hoover (1988); Pitcher and Calkins (1979); Ronald et al. (1982).

Harbor Seal (*Phoca vitulina*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (kg)	A M (> 7 yrs) A F (> 7 yrs)	84.6 ± 11.3 SD 76.5 ± 17.7 SD		Gulf of Alaska	Pitcher & Calkins, 1979	
	J M 2 yrs J M 4 yrs J M 6 yrs A M 8 yrs A M 12 yrs A M 16 yrs A M 24 yrs	49 70 84 95 110 120 124		Aleutian Ridge and Pribilof Islands, Bering Sea, Alaska	Ashwell-Erickson & Elsner, 1981	1
	J F 2 yrs J F 4 yrs J F 6 yrs A F 8 yrs A F 12 yrs A F 16 yrs A F 24 yrs	40 56 67 76 90 101 112				
	neonate M neonate F	12.0 ± 0.51 SE 11.5 ± 0.31 SE		Alaska	Pitcher & Calkins, 1979	
	at weaning B	24.0		British Columbia, Canada	Bigg, 1969a	2
Pup Growth Rate (g/day)	birth to weaning M F	 520 790		Gulf of St. Lawrence/island marine	Rosen, 1989	
Metabolic Rate (lO_2/kg-day)	J B resting A F resting	7.3 6.6		California/lab	Davis et al., 1985	3

Harbor Seal (*Phoca vitulina*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Metabolic Rate (kcal/kg-day)	1 to 4 yrs old/ basal	57.5		Bering Sea, Alaska	Ashwell-Erickson & Elsner, 1981	
	A F basal A M basal	24.3 22.4			estimated	4
	A F free-living A M free-living	131 129	(57 - 300) (56 - 296)		estimated	5
Food Ingestion Rate (g/g-day)	A B	0.05		e Canada/marine	Boulva and McLaren, 1979	
	A B A F lact./gest.	0.06 to 0.08 0.10		review of several studies	Ashwell-Erickson & Elsner, 1981	
	J B 1st year	0.13		Bering Sea (1 harbor & 1 spotted seal)	Ashwell-Erickson & Elsner, 1981	
Water Ingestion Rate (g/g-day)	A B	0.0048	0.0028 - 0.0091	seawater ingestion (most water obtained from food)	Depocas et al., 1971	
	A B	0.064			estimated	6
Inhalation Rate (m^3/day)	A M A F	18.6 17.2			estimated	7
Surface Area (cm^2)	A M A F	19,620 18,380			estimated	8

Harbor Seal (*Phoca vitulina*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
walleye pollock	3.7	27.3	32.2	1.3	Washington/	Everitt et al., 1981	
English sole	37.0	0.0	27.0	0	coastal island		
shiner perch	0.0	0.0	0.5	63.6			
Pacific herring	0	54.6	3.9	28.6	(% of total otoliths		
Pacific cod	0	0	10.1	0	recovered from scat		
rex sole	37	9.1	2.9	0	samples)		
Pacific tomcod	3.7	0	4.7	0			
rockfish	3.7	0	4.7	0			
Dover sole	3.7	0	3.4	2.6			
Petrale sole	7.4	0	1.8	0			
other fish	3.8	9.0	8.8	3.9			
octopus		17.6	17.7	30.4	Kodiak Island, Alaska/	Pitcher & Calkins, 1979	
salmon		5.4	0.0	0.0	coastal marine		
capelin		20.3	4.8	5.4			
Pacific cod		6.8	8.1	10.7	(% frequency of occurrence;		
walleye pollock		12.2	9.7	14.3	stomach contents)		
Pacific sandlance		4.1	21.0	0.0			
squid & octopus		20			Gulf of Alaska/	Pitcher, 1980	
shrimp, crabs		3.7			coastal marine		
herring		6.4					
salmonids		4.4			(% wet volume; stomach		
osmerids		22.5			contents)		
cod, tomcod,		26.0					
walleye, pollock					all seasons combined		
other		14.1					

Harbor Seal (*Phoca vitulina*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Foraging Radius (km)	A B A B	5 km 30 to 55 km	unknown unknown	California/Bay Washington/Columbia River	Stewart et al., 1989 Beach et al., 1985	9 10
Population Density (N/ha)	summer	0.0305	0.00394 - 0.0611 highly clumped distrib.	Maine/coastal marine throughout range and habitats	Richardson, 1981 Pitcher and Calkins, 1979	
Litter Size		1		throughout range and habitats	Hoover, 1988	
Litters /Year		1		throughout range and habitats	Hoover, 1988	
Months Gestation		10.5 to 11		NS/NS	FAO Adv. Comm., 1976	11
Age at Weaning	B B	30 days 35 days		e Canada/marine c California/coastal marine	Boulva & McLaren, 1979 Slater & Markowitz, 1983	
Age at Sexual Maturity (years)	F M F M	5.5 ± 0.23 SE 3 to 4 6	4 - 9 5 - 7	Gulf of Alaska/coastal marine e Canada/marine	Pitcher & Calkins, 1979 Boulva & McLaren, 1979	
Annual Mortality Rates (percent)	A B birth to 4 yrs 4 to 5 yrs old 7 to 14 yrs old $\geq$ 20 yrs old	17.5 77/4 yrs 11/yr 8 to 9/yr 14/yr		e Canada/marine Gulf of Alaska/coastal marine	Boulva & McLaren, 1979 Pitcher & Calkins, 1979	12
Longevity	A B A M A F		< 30 < 26 < 31	e Pacific/NS Gulf of Alaska/coastal marine	Newby, 1978 Pitcher & Calkins, 1979	

Harbor Seal (*Phoca vitulina*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early April		July	Nova Scotia, Canada	Boulva & McLaren, 1979	
		February		Mexico	Bigg, 1969b	13
		July		Bering Sea	Bigg, 1969b	13
Parturition	mid-May	mid-June	late June	Tugidak Island, Alaska	Pitcher & Calkins, 1979	
	late April		early May	c California	Riedman, 1990	
	early February			Mexico		
	late June		September	Canada		
	May	early June	June	Washington	Johnson & Jeffries, 1983	
	August		September	Washington, Puget Sound		
Molt	early June		early September	Scotland	Thompson & Rothery, 1987	14
	late June	late July	September/October	Gulf of Alaska	Pitcher & Calkins, 1979	

1 Estimated from graph of growth curve.
2 Cited in Boulva and McLaren (1979). Weight doubled from birth.
3 Juvenile is a yearling; weight 33 kg. Adult female weight 63 kg.
4 Estimated using equation 3-43 (Boddington, 1978) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
5 Estimated using equation 3-47 (Nagy, 1987) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived. Mean values are somewhat higher than is consistent with food ingestion rate estimates and data from the spotted seal (see Appendix).
6 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
7 Estimated using equation 3-20 (Stahl, 1967) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
8 Estimated using equation 3-22 (Stahl, 1967) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
9 Satellite telemetry of one seal. Foraging radius depends on distribution and abundance of prey.
10 Seventy-five percent of 58 seals radio-tagged in the Columbia River were relocated at haul-out sites 30 to 55 km away. Cited in Hoover (1988).
11 Cited in Ronald et al. (1982).
12 Postweaning mortality.
13 Cited in Hoover (1988).
14 Nineteen to 33 days to complete molt.

References (including Appendix)

Allen, S. G.; Huber, H. R.; Ribic, C. A.; et al. (1989) Population dynamics of harbor seals in the Gulf of the Farallones, California. Calif. Fish Game 75: 224-232.

Angell-James, J. E.; Elsner, R.; de Burgh Daly, M. (1981) Lung inflation: effects on heat rate, respiration, and vagal afferent activity in seals. Am. J. Physiol. 240: H190-H198.

Ashwell-Erickson, S.; Elsner, R. (1981) The energy cost of free existence for Bering Sea harbor and spotted seals. In: Hood, D. W.; Calder, J. A., eds. The Eastern Bering Sea shelf: oceanography and resources. v. 2. Washington, DC: Department of Commerce; pp. 869-899.

Ashwell-Erickson, S.; Elsner, R.; Wartzol, D. (1979) Metabolism and nutrition of Bering Sea harbor and spotted seals. Proc. Alaska Sci. Conf. 29: 651-665.

Beach, R.J.; Geiger, A.; Jeffries, S. J., et al. (1985) Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980-1982. Seattle, WA: Third Ann. Rept. to U.S. Dept. Commerce, NOAA, Natl. Mar. Fish. Serv.

Bigg, M. A. (1969a) The harbour seal in British Columbia. Fish. Res. Board Can.; Bull. 172.

Bigg, M. A. (1969b) Clines in the pupping season of the harbour seal, *Phoca vitulina*. J. Fish. Res. Board Can. 26: 449-455.

Boddington, M. J. (1978) An absolute metabolic scope for activity. J. Theor. Biol. 75: 443-449.

Boulva, J.; McLaren, I. A. (1979) Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. Quebec, Canada: Fish. Res. Board Can. Bull. 200.

Brown, R. F.; Mate, B. R. (1983) Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Nearts and Tillamook Bays, Oregon. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 81: 291-301.

Brown, R. F.; Jeffries, S. J.; Harvey, J. T. (1989) Seasonal abundance and winter feeding ecology of harbor seals in the Columbia River (abstract). In: 8th Biennial Conference on the Biology of Marine Mammals; December 7-11, 1989; Pacific Grove, CA; p. 9.

Bryden, M. M. (1972) Growth and development of marine mammals. In: Harrison, R. J., ed. Functional anatomy of marine mammals. New York, NY: Academic Press; pp. 2-79.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Craig, A. B., Jr.; Pasche, A. (1980) Respiratory physiology of freely diving harbor seals (*Phoca vitulina*). Physiol. Zool. 53: 419-432.

da Silva, J.; Neilson, J. D. (1985) Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42: 1439-1442.

Davis, R. W.; Williams, T. M.; Kooyman, G. L. (1985) Swimming metabolism of yearling and adult harbor seals (*Phoca vitulina*). Physiol. Zool. 58: 590-596.

Depocas, F.; Hart, J. S.; Fisher, H. D. (1971) Sea water drinking and water flux in starved and in fed harbor seals, *Phoca vitulina*. Can. J. Physiol. Pharmacol. 49: 53-62.

Everitt, R. D.; Gearin, P. J.; Skidmore, J. S.; et al. (1981) Prey items of harbor seals and California sea lions in Puget Sound, Washington. Murrelet 62: 83-86.

Food and Agriculture Organization (FAO) of the United Nations, A. C. on Marine Resources Research. (1976) Mammals in the seas. Ad Hoc Group III on seals and marine otters, draft report. In: Symposium: Scientific consultation on marine mammmals; August 13 to September 9, 1976; Food and Agric. Advis. Comm. Mar. Resour. Res., Mar. Mammal, Sci. Consult. Organ. of U.N., Bergen, Norway.

Harkonen, T. J. (1988) Food-habitat relationship of harbour seals and black cormorants in Skagerrak and Kattegat. J. Zool. (London) 214: 673-681.

Harvey, J. T. (1989) Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. J. Zool. (Lond.) 219: 101-111.

Hoover, A. A. (1988) Harbor seal, *Phoca vitulina*. In: Lentfer, J. W., ed. Selected marine mammals of Alaska: species accounts with research and management recommendations. Washington, DC: Marine Mammal Commission; pp. 125-157.

Innes, S.; Lavigne, D. M.; Earle, W. M.; et al. (1987) Feeding rates of seals and whales. J. Anim. Ecol. 56: 115-130.

Irving, L. (1972) Arctic life of birds and mammals including man. New York, NY: Springer-Verlag.

Johnson, M. L.; Jeffries, S. J. (1977) Population evaluation of the harbour seal (*Phoca vitulina richardii*) in the waters of the state of Washington. U.S. Mar. Mammal Comm.; Rep. MMC-75/05.

Johnson, M. L.; Jeffries, S. J. (1983) Population biology evaluation of the harbor seal (*Phoca vitulina richardii*) in the waters of the State of Washington: 1976-1977. Tacoma, WA: University of Puget Sound; MMC-76/25.

Jones, R. E. (1981) Food habits of smaller marine mammals from northern California. Proc. Calif. Acad. Sci. 42: 409-433.

Klinkhart, E. G. (1967) Birth of a harbor seal pup. J. Mammal. 48: 677.

Lawson, J. W.; Renouf, D. (1987) Bonding and weaning in harbor seals, *Phoca vitulina*. J. Mammal. 68: 445-449.

Ling, J. K. (1970) Pelage and molting in wild animals with special reference to aquatic forms. Q. Rev. Bio. 45: 16-54.

Ling, J. K. (1974) The integument of marine mammals. In: Harrison, R. J., ed. Functional anatomy of marine mammals: v. 2. New York, NY: Academic Press; pp. 1-44.

Lowry, L. F.; Frost, K. J. (1981) Feeding and trophic relationships of phocid seals and walruses in the Eastern Bering Sea. In: Hood, D. W.; Calder, J. A., eds. The Eastern Bering Sea shelf: oceanography and resources: v. 2. Washington, DC: Department of Commerce; pp. 813-824.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Mono. 57: 111-128.

Newby, T. C. (1973) Observations on the breeding behavior of the harbor seal in the State of Washington. J. Mammal. 54: 540-543.

Newby, T. C. (1978) Pacific harbor seal. In: Haley, D., ed. Marine mammals of eastern north Pacific and arctic waters. Seattle, WA: Pacific Search Press; pp. 184-191.

Payne, P. M.; Schneider, D. C. (1984) Yearly changes in abundance of harbor seals, *Phoca vitulina*, at a winter haul-out site in Massachusetts. Fish. Bull. 82: 440-442.

Payne, P. M.; Selzer, L. A. (1989) The distribution, abundance and selected prey of the harbor seal, *Phoca vitulina concolor*, in southern New England. Mar. Mammal. Sci. 5: 173-192.

Perez, M. A. (1990) Review of marine mammals population and prey information for Bering Sea ecosystem studies. Washington, DC: U.S. Dept. Commerce, Nat. Oceanic Atm. Admin., Nat. Mar. Fish. Serv.; NOAA Tech. Mem. NMFS F/NWC-186.

Perry, E. (1989) Evidence for polygyny in harbour seals, *Phoca vitulina*. In: 8th Biennial conference on the biology of marine mammals; December; Pacific Grove, CA.

Pierotti, R.; Pierotti, D. (1980) Effects of cold climate on the evolution of pinniped breeding systems. Evolution 34: 494-507.

Pitcher, K. W. (1977) Population productivity and food habits of harbor seals in the Prince William Sound-Copper River Delta area, Alaska. Final report to U. S. Marine Mammal Commission No. MMC-75103. USDC NTIS. PB-226 935.

Pitcher, K. W. (1980) Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 78: 544-549.

Pitcher, K. W.; Calkins, D. G. (1979) Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final report. Outer Continental Shelf Environmental Assessment Program Research Unit 229, Contract No. 03-5-002-69.

Pitcher, K. W.; McAllister, D. C. (1981) Movements and haulout behavior of radio-tagged harbor seals, *Phoca vitulina*. Can. Field-Nat. 95:292-297.

Power, G.; Gregoire, J. (1978) Predation by freshwater seals on the fish community of lower Seal Lake, Quebec. J. Fish. Res. Board Can. 35: 844-850.

Renouf, D. (1989) Weight increases in harbour seals in spite of reduced food intake and heightened thermal demands: adjustable metabolism? In: 8th Biennial Conference on the Biology of Marine Mammals; December; Pacific Grove, CA.

Richardson, D. T. (1973) Distribution and abundance of harbor and gray seals in Acadia National Park. Final report to National Park Service and Maine Department of Sea and Shore Fisheries. State of Maine Contract No. MM4AC009.

Richardson, D. T. (1981) Feeding habits and population studies of Maine's harbor and gray seals. Natl. Geogr. Soc. Res. Rep. 13: 497-502.

Riedman, M. (1990) The pinnipeds: seals, sea lions, and walruses. Berkeley, CA: University of California Press.

Roffe, T. J.; Mate, B. R. (1984) Abundances and feeding habits of pinnipeds in the Rogue River, Oregon. J. Wildl. Manage. 48: 1262-1274.

Ronald, K.; Selley, J.; Healey, P. (1982) Seals. In: Chapman, J. A.; Feldhammer, G. A., eds. Wild mammals of North America. Baltimore, MD: Johns Hopkins University Press; pp. 769-827.

Rosen, D. A. (1989) Neonatal growth rates and behaviour in the Atlantic harbour seal, *Phoca vitulina* (abstract). In: 8th Biennial Conference on the Biology of Marine Mammals; December 7-11, 1989; Pacific Grove, CA; p. 57.

Scheffer, V. B.; Slipp, J. W. (1944) The harbor seal in Washington state. Am. Midl. Nat. 32: 373-416.

Schneider, D. C.; Payne, P. M. (1983) Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. J. Mammal. 64: 518-520.

Selzer, L. A.; Early, G.; Fiorelli, P. M.; et al. (1986) Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concolor*, in southern New England. Fish. Bull. 84: 217-220.

Shaffer, K. E. (1989) Seasonal and size variations in diets of harbor seals, *Phoca vitulina* (abstract). In: 8th Biennial Conference on the Biology of Marine Mammals; December 7-11, 1989; Pacific Grove, CA; p. 62.

Slater, L. M.; Markowitz, H. (1983) Spring population trends in *Phoca vitulina richardi* in two central California coastal areas. Calif. Fish Game 69: 217-226.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Stewart, B. S.; Leatherwood, S.; Yochem, P. K.; et al. (1989) Harbor seal tracking and telemetry by satellite. Mar. Mamm. Sci. 5: 361-375.

Stutz, S. S. (1966) Moult and pelage patterns in the Pacific harbor seal, *Phoca vitulina* [master's thesis]. Vancouver, Canada: University of British Columbia.

Thompson, P; Rothery, P. (1987) Age and sex differences in the timing of moult in the common seal, *Phoca vitulina*. J. Zool. (London) 212: 597-603.

Wilson, S. C. (1978) Social organization and behavior of harbor seals *Phoca vitulina concolor* in Maine. Final report to Marine Mammal Commission, Contract No. GPO PB 280-3188. NTIS PB 280 188.

2.2.7. Deer Mouse (deer and white-footed mice)

Order *Rodentia*, Family *Muridae* (Genus *Peromyscus*).[h] New world mice (family Muridae) are small, ground-dwelling rodents that live in a large variety of habitats including woodlands, prairies, rocky habitats, tundra, and deserts. All are nocturnal and are preyed on by owls, hawks, snakes, and carnivorous mammals. Most species eat primarily seeds, but some also regularly eat small invertebrates. Many species store food. The genus *Peromyscus* is the most widespread and geographically variable of North American rodents (MacMillen and Garland, 1989).

Selected species

The deer mouse *(Peromyscus maniculatus)* is primarily granivorous and has the widest geographic distribution of any *Peromyscus* species (Millar, 1989; Brown and Zeng, 1989). It is resident and common in nearly every dry-land habitat within its range, including alpine tundra, coniferous and deciduous forest, and grasslands as well as deserts. There are many recognized subspecies or races of the deer mouse associated with different locations or insular habitats, including *artemisiae, austerus, bairdii, balaclavae, blandus, borealis, carli, cooledgei, gambelii, gracilis, labecula, maniculatus, oreas, nebrascensis, nubiterrae, rufinus,* and *sonoriensis* (MacMillen and Garland, 1989; Millar, 1982)

Body size. Deer mice range from 7.1 to 10.2 cm in length, with a 5.1 to 13 cm tail, and adults weigh from 15 to 35 g (Burt and Grossenheider, 1980; see table). Body size varies somewhat among populations and subspecies throughout the species' range. Body weight also varies seasonally, being lower in autumn and winter and a few grams higher in spring and summer (Zegers and Merritt, 1988). There may (Fleharty et al., 1973) or may not (Millar and Schieck, 1986) be seasonal differences in fat content.

Habitat. Deer mice inhabit nearly all types of dry-land habitats within their range: short-grass prairies, grass-sage communities, coastal sage scrub, sand dunes, wet prairies, upland mixed and cedar forests, deciduous forests, ponderosa pine forests, other coniferous forests, mixed deciduous-evergreen forests, juniper/piñon forests, and other habitats (Holbrook, 1979; Kaufman and Kaufman, 1989; Ribble and Samson, 1987; Wolff and Hurlbutt, 1982). Few studies have found microhabitat features that distinguish the deer mouse, and some studies have come to different conclusions regarding habitat structure preferences (Ribble and Samson, 1987). For example, Vickery (1981) found that deer mice appeared to prefer areas with moderate to heavy ground and mid-story cover to more open ground areas, whereas others have found more deer mice in more open than in more vegetated areas (see Kaufman and Kaufman, 1989).

Food habits. Deer mice are omnivorous and highly opportunistic, which leads to substantial regional and seasonal variation in their diet. They eat principally seeds, arthropods, some green vegetation, roots, fruits, and fungi as available (Johnson, 1961; Menhusen, 1963; Whitaker, 1966). The nonseed plant materials provide a significant

---

[h] *Peromyscus* is considered a member of the family Cricetidae by some mammalogists.

proportion of the deer mouse's daily water requirements (MacMillen and Garland, 1989). Food digestibility and assimilation for most of their diet have been estimated to be as high as 88 percent (Montgomery, 1989). Deer mice may cache food during the fall and winter in the more northern parts of their range (Barry, 1976; Wolff, 1989). They are nocturnal and emerge shortly after dark to forage for several hours (Marten, 1973).

***Temperature regulation*.** The deer mouse has a metabolic rate about 1.3 times higher than the other species in the genus (MacMillen and Garland, 1989; Morris and Kendeigh, 1981; see table). Its metabolic rate is substantially higher in winter than in summer (Morris and Kendeigh, 1981; Stebbins, 1978; Zegers and Merritt, 1988). Outside the thermoneutral zone (25 to 35°C), metabolic rate varies according to the following equation:

$$V_{O2} = 0.116 - 0.003(T_a) + 0.0304\ (V^{0.5})$$

where V_{O2} = volume oxygen consumed (ml/g-min); T_a = ambient temperature; and V = wind speed (Chappell and Holsclaw, 1984). Deer mice can enter torpor (body temperature, 19 to 30°C) to reduce metabolic demands in the winter and also in response to brief food shortages (Tannenbaum and Pivorun, 1988, 1989). The deer mouse uses nonshivering thermogenesis (NST) to quickly awaken from torpor and to maintain body temperature during the winter (Zegers and Merritt, 1987). The deer mouse may burrow in soils to assist thermoregulation; one study measured the burrow dimensions to be 24 cm deep (range 13 to 50 cm) and 132 cm long (range 30 to 470 cm) (Reynolds and Wakkinen, 1987).

Breeding activities and social organization. The duration of the reproductive season varies with latitude and longitude according to the regression equation:

$$Y = -33.0 + 2.79\ X + 0.0748\ Z - 0.0370\ X^2$$

where Y = duration of the breeding season in weeks, X = latitude, and Z = longitude (r = 0.58; Millar, 1989). Lactating females have longer gestation periods than nonlactating females. Newborn deer mice are highly altricial (Layne, 1968). Several studies have indicated that daily food consumption increases over 15 percent during early pregnancy and more than doubles during lactation (Glazier, 1979; Millar, 1975, 1978, 1979, 1982, 1985; Millar and Innes, 1983; Stebbins, 1977). Deer mice are promiscuous; in one study, 19 to 43 percent of litters resulted from multiple inseminations (Birdsall and Nash, 1973, as cited in Millar, 1989).

***Home range and resources*.** Deer mice tend to occupy more than one nest site, most frequently in tree hollows up to 8 m from the ground (Wolff and Durr, 1986) but also among tree roots and under rocks and logs (Wolff and Hurlbutt, 1982; Wolff, 1989). At low densities, home ranges are maintained by mutual avoidance, but at higher densities, females may defend a core area or territory (Wolff, 1989). The home range of female deer mice encompasses both their foraging areas and their nests. Male home ranges are larger and overlap the home ranges of many females (Cranford, 1984; Taitt, 1981; Wolff, 1985a, 1986; Wolff et al., 1983).

***Population density*.** **Population density varies considerably over space and time and is often positively correlated with food abundance (Taitt, 1981; Wolff, 1989), moisture content of plants (Bowers and Smith, 1979), and vegetative cover (van Horne, 1982) as well as season (Montgomery, 1989; Taitt, 1985). Interspecific competition also can play a role in determining population densities (Kaufman and Kaufman, 1989).**

***Population dynamics*.** **Although laboratory and field studies have demonstrated that females can produce their first litter by 3 months of age, females of the more northern populations do not mature under natural conditions until the spring after the year of their birth. First litters are consistently smaller than subsequent litters (Millar, 1989), and latitude and elevation explain a significant amount of the variation in litter size among *P. maniculatus* populations (Smith and McGinnis, 1968, as cited in Millar, 1989). Millar (1989) estimated the relationship between litter size and latitude and longitude to be**

$$Y = -1.62 + 0.0103X + 0.106Z + 0.0004X^2 - 0.0005Z^2$$

where Y is the mean litter size; X, the latitude; and Z, the longitude. The largest litters are produced in northwestern North America. Pups wean within about 3 weeks, and females may have up to four litters per year in the more southern parts of the species' range (Millar, 1989). Mortality rates are high, and most deer mice live for less than 1 year (Millar and Innes, 1983).

Similar species (from general references)

- **The cactus mouse (*Peromyscus eremicus*), almost the same size as the deer mouse (8.1 to 9.1 cm; 17 to 40 g), is found only in low deserts of the extreme southwest and Mexico. It may feed on green vegetation, seeds, and berries and can climb trees for food.**

- **The California mouse (*Peromyscus californicus*) (9.6 to 11.7 cm; 42 to 50 g) is found in southwestern California and lives among oaks and dense chaparral. It stores acorns in nests made of twigs and sticks.**

- **The canyon mouse (*Peromyscus crinitus*) (7.6 to 8.6 cm) is limited to the western United States. It lives in rocky canyons and on lava-covered slopes, nesting among rocks.**

- **The oldfield mouse (*Peromyscus polionotus*), smaller than the deer mouse (4.1 to 6.1 cm), is limited to the extreme southeastern United States, where it inhabits sandy beaches and fields and feeds on seeds and berries. Females may be territorial during the breeding season.**

- **The white-footed mouse (*Peromyscus leucopus*) is approximately the same size as the deer mouse (9.1 to 10.7 cm; 14 to 31 g). Its range extends north into Canada and west to Arizona but does not extend as far north and west as the deer mouse's range. Like the deer mouse, the white-footed mouse's diet consists mainly of arthropods, seeds, and other vegetation, and it usually nests off the ground. It is most abundant in habitat that includes a** canopy, such as brushy fields and deciduous woodlots in northern regions and riparian areas and ravines in prairie and semidesert regions.

- The cotton mouse (*Peromyscus gossypinus*) (9.1 to 11.7 cm; 28 to 51 g) is found in the southeastern United States where it inhabits wooded areas, swampland, stream banks, and field edges. This tree climber nests in trees, under logs, and in buildings.

- The brush mouse (*Peromyscus boylii*) (9.7 to 10.7 cm; 22 to 36 g) is limited to chaparral and rocky areas of the arid and semiarid west and southwest United States. A good climber, it lives under rocks and debris and in crevices. It feeds on pine nuts, acorns, seeds, and berries.

General references

Burt and Grossenheider (1980); Kirkland and Lane (1989); Millar (1985, 1989); Wolff (1989).

Deer Mouse (*Peromyscus maniculatus*)

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A M A F	22 20		North America	Millar, 1989	
	A M A F	15.7 14.8		NS (*austerus*)	Fordham, 1971	1
	A M A F	22.3 21.1		NS (*blandus*)	Dewsbury et al., 1980	1
	A B	19.6 ± 0.71 SE		New Hampshire	Schlesinger & Potter, 1974	
	A F nonbreed. A F gestat. A F lactat.	20.3 ± 0.42 SE 31.5 ± 0.43 SE 24.5 ± 0.37 SE		NS (*borealis*) lab	Millar & Innes, 1983	
	neonate neonate	1.8 1.7 ± 0.02 SE	1.6 - 2.8	North America Alberta, Canada	Millar, 1989 Millar, 1989	
	at weaning at weaning	8.8 9.3 ± 0.10 SE	7.7 - 11.2	North America Northwest Territories, Canada	Millar, 1989 Millar, 1979	
Pup Growth Rate (g/day)	B	0.38 ± 0.01 SE	0.30 - 0.95	Alberta, Canada (*nebrascensis*)	Millar, 1985	
	M F	0.27 ± 0.06 SE 0.22 ± 0.05 SE		Alberta, Canada (*borealis*)	Millar & Innes, 1983	2
Metabolic Rate (lO_2/kg-day)	F resting	50	40 - 61	North America	MacMillen & Garland, 1989	
	M avg daily: winter spring summer	 138 ± 5.3 SE 102 ± 7.2 SE 75 ± 3.4 SE		Alberta, Canada lab	Stebbins et al., 1980	3

Deer Mouse (*Peromyscus maniculatus*)

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Metabolic Rate (kcal/kg-day)	M avg daily:			Alberta, Canada lab	Stebbins et al., 1980	3
	winter	668 ± 25 SE				
	spring	623 ± 35 SE				
	summer	360 ± 17 SE				
	B free-living:			Illinois lab	Morris & Kendeigh, 1981	4
	winter	790				
	summer	592				
	A M free-living	547	(259 - 1,153)		estimated	5
	A F free-living	574	(271 - 1,212)			
Food Ingestion Rate (g/g-day)	A F nonbreed.	0.19		Manitoba, Canada (*maniculatus*) lab	Millar, 1979	6
						7
	A F nonbreed.	0.18		Alberta, Canada (*borealis*) lab	Millar & Innes, 1983	
						6
						7
	A F lactating	0.45		Manitoba, Canada (*maniculatus*) lab	Millar, 1979	
						8
	A F lactating	0.38		Alberta, Canada (*borealis*) lab	Millar & Innes, 1983	
						9
	A F nonbreed.	0.19		Virginia lab	Cronin & Bradley, 1988	
	A M nonbreed.	0.22				
	J M	0.21 ± 0.01 SE		South Dakota lab	Nelson & Desjardins, 1987	
Water Ingestion Rate (g/g-day)	A B	0.19		(*sonoriensis*) lab	Ross, 1930	10
	A B	0.19	0.123 - 0.287	Illinois (*bairdii*) lab	Dice, 1922	11
	J M	0.34 ± 0.02 SE		South Dakota lab	Nelson & Desjardins, 1987	12
		0.15			estimated	13
Inhalation Rate (m^3/day)	A M	0.025			estimated	14
	A F	0.023				
Surface Area (cm^2)	A M	91			estimated	15
	A F	86				

Deer Mouse (*Peromyscus maniculatus*)

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
nuts/seeds		0	24	23	Virginia (*nubiterrae*)/ oak-maple-hickory forest	Wolff et al., 1985	
arthropods		56	30	46			
Lepidopt. larvae		4	trace	2			
Lepidopt. adults		3	26	7	(% frequency of occurrence; stomach contents)		
green veg.		5	12	18			
fungus		7	trace	1			
fruit		25	4	1			
unknown		1	4	3			
Lepidopt. larvae	20.6	34.5	16.7	4.8	Indiana/several habitats	Whitaker, 1966	
corn	4.1	4.2	3.2	8.7			
misc. veg.	15.8	3.1	8.0	13.4			
wheat seeds	6.5	1.6	3.2	23.7	(% volume; stomach contents)		
unident. seeds	5.4	5	8.8	8.3			
green veg.	7.6	0	4.3	3.7			
Echinochloa seeds	0	1.2	6.4	0			
Coleoptera	3.9	5.3	5.1	1.4			
soybeans	13.4	3.1	6.9	10.7			
Hemiptera	1.3	2.7	4.2	0.9			
beetles	14.6	23.8	9.4	4.9	Colorado/short grass prairie	Flake, 1973	
grasshoppers	6.4	4.2	6.4	2.5			
leafhoppers	13.3	1.8	1.9	2.5	(% volume by a ranking method; stomach contents)		
Lepidopterans	21.7	12.7	1.5	1.8			
spiders	2.6	2.7	2.5	0.3			
seeds	22.5	25.9	56.8	65.4			
forbs	4.7	10.0	5.6	4.3			
grasses & sedges	4.0	2.6	2.8	4.8			
shrubs	3.8	1.4	0.8	2.6			

Deer Mouse (*Peromyscus maniculatus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	A M summer A F summer	0.039 ±0.0054 SD 0.027 ±0.0047 SD		Utah/subalpine meadow snowfree	Cranford, 1984	
	A M winter A F winter	0.019 ±0.0065 SD 0.014 ±0.0050 SD		Utah/subalpine meadow snowbound	Cranford, 1984	
	B M B F	0.058 ± 0.006 SE 0.061 ± 0.005 SE	0.054 - 0.065 0.054 - 0.072	Virginia/mixed deciduous forest	Wolff, 1985a	
	A M A F	0.10 ± 0.0063 SE 0.075 ±0.0063 SE		Oregon/ponderosa pines	Bowers & Smith, 1979	
	A M A F	0.128 ± 0.012 SE 0.094 ±0.0013 SE		Idaho/(*artemisiae-sarcobatus*) desert	Bowers & Smith, 1979	
Population Density (N/ha)	B B	0.19		Arizona/desert	Brown & Zeng, 1989	
	A B summer	2.8		Colorado/subalpine meadows	Vaughn, 1974	
	B B summer B B winter		12.8 - 22.4 3.4 - 8.4	Utah/subalpine meadow	Cranford, 1984	
	A B		12.7 - 45.5	British Columbia, Canada/burnt slash	Sullivan, 1979	
	B B	12 ± 6.7 SD	3.9 - 28	Montana/understory near river	Metzgar, 1979	
Litter Size		3.4		Virginia (*nubiterrae*)/NS	Wolff, 1985b	
		4.4	3.0 - 6.4	average for North America/NS	Millar, 1989	
		5.1 ± 0.14 SE	1 - 8	Alberta, Canada (*nebrascensis*)/NS	Millar, 1985	
Litters/Year		2.4		average for North America/NS	Millar, 1989	
		1.9 ± 0.1 SE		Alberta, Canada (*borealis*)/various alpine	Millar & Innes, 1983	

Deer Mouse (*Peromyscus maniculatus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Days Gestation	F non-lact. F lactating	23.6 26.9		average for United States/NS	Millar, 1989	
	F non-lact. F lactating	22.4 ± 0.1 SE 24.1 ± 0.3 SE	22 - 23 22 - 27	Kansas/NS	Svendsen, 1964	16
	F non-lact. F lactating	25.5 ± 0.3 SE 29.5 ± 1.4 SE	23 - 26 24 - 35	Alberta, Canada (*nebrascensis*)/lab	Millar, 1985	
Age at Weaning (days)	B	20.2	16 - 25	average for North America/NS	Millar, 1989	
	B	24.9		Alberta, Canada (*borealis*)/various alpine	Millar & Innes, 1983	
	B	17.5		Colorado/NS	Halfpenny, 1980	16
Age at Sexual Maturity	M F	35 days 60 days		Alberta, Canada (*nebrascensis*)/lab	Millar, 1985	
Mortality Rates	A F winter A M winter J F winter J M winter	100%/winter 33%/winter 56%/winter 70%/winter		Alberta, Canada (*borealis*)/ various alpine	Millar & Innes, 1983	
	A B summer J B summer	20%/2 weeks 19%/2 weeks		Alberta, Canada (*borealis*)/ various alpine	Millar & Innes, 1983	
Longevity	B B	< 1 yr		Alberta, Canada (*borealis*)/ various alpine	Miller & Innes, 1983	

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating	April		August	Massachusetts	Drickamer, 1978	16
	November		April	Texas	Blair, 1958	16
	March		October	Virginia (*nubiterrae*)	Wolff, 1985b	16
	May		August	California	Dunmire, 1960	16
Dispersal		spring (males)		Vancouver, Canada	Fairbairn, 1977	

Deer Mouse (*Peromyscus maniculatus*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Torpor		winter		northern parts of range	Tannenbaum & Pivorun, 1989	

1 Cited in Montgomery (1989).
2 Growth rate of "newly emerged" pups, soon after leaving the nest.
3 Temperatures during winter averaged -17.7°C (-6 to -22°C); during spring averaged 14.5°C (8 to 22°C); during summer 20.6°C (14 to 32°C).
4 Estimated by authors from laboratory-derived model assuming no reproduction, molt, or weight change and assuming summer temperatures averaged 17.5°C above ground and 20.2°C in burrows and winter temperatures averaged -3°C above ground and 10.7°C in burrows.
5 Estimated using equation 3-48 (Nagy, 1987) and body weights from Millar (1989).
6 Diet of rat chow with 3 percent water content and 4.5 kcal/g dry weight.
7 Diet of Purina lab chow no. 5001; composition not specified.
8 Diet of lab chow; composition not specified.
9 Diet of lab chow with 8 to 10 percent water content.
10 Mean varied by subspecies; *sonoriensis, eremicus, gambelii*, and *fraterculus* tested. Dry diet prepared in lab, probably less than 10 percent water content; air temperature 21 to 24°C.
11 Dry air at 32 to 34°C; diet of wheat and peanuts, about 10 percent water content.
12 Temperature 20°C ± 2°C; diet of lab chow with 8 to 10 percent water content.
13 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Millar (1989).
14 Estimated using equation 3-20 (Stahl, 1967) and body weights from Millar (1989).
15 Estimated using equation 3-22 (Stahl, 1967) and body weights from Millar (1989).
16 Cited in Millar (1989).

References (including Appendix)

Abbott, K. D. (1974) Ecotypic and racial variation in the water and energy metabolism of *Peromyscus maniculatus* from the western United States and Baja California, Mexico [Ph.D. dissertation]. Irvine, CA: University of California.

Agnew, W. J.; Uresk, D. W.; Hansen, R. M.; et al. (1988) Arthropod consumption by small mammals on prairie dog colonies and adjacent ungrazed mixed grass prairie in western South Dakota. In: Uresk, D. W.; Schenbeck, G. L.; Cefkin, R., tech. coords. Eighth Great Plains wildlife damage control workshop proceedings; April 28-30, 1987; Rapid City, South Dakota. Fort Collins, CO: U.S. Dept. Agr., Forest Serv., Rocky Mountain Forest and Range Experiment Station; pp. 81-87.

Barry, W. J. (1976) Environmental effects on food hoarding in deermice (*Peromyscus*). J. Mammal. 57: 731-746.

Birdsall, D. A.; Nash, D. (1973) Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). Evolution 27: 106-110.

Blair, W. F. (1940) A study of prairie deer mouse populations in southern Michigan. Am. Midl. Nat. 24: 273-305.

Blair, W. F. (1958) Effects of x-irradiation of a natural population of deer-mouse (*Peromyscus maniculatus*). Ecology 39: 113-118.

Bowers, M. A.; Smith, H. D. (1979) Differential habitat utilization by sexes of the deermouse, *Peromyscus maniculatus*. Ecology 60: 869-875.

Brower, J. E.; Cade, T. J. (1966) Ecology and physiology of *Napaeozapus insignis* (Miller) and other woodland mice. Ecology 47: 46-63.

Brown, J. H.; Zeng, Z. (1989) Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. Ecology 70: 1507-1525.

Burt, W. H.; Grossenheider, R. P. (1980) A field guide to the mammals of North America north of Mexico. Boston, MA: Houghton Mifflin Co.

Calder, W. A.; Braun, E. J. (1983) Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. 244: R601-R606.

Chappell, M. A.; Holsclaw, D. S., III (1984) Effects of wind on thermoregulation and energy balance in deer mice (*Peromyscus maniculatus*). J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 154: 619-625.

Cook, J. C.; Topping, M. S.; Stombaugh, T. A. (1982) Food habits of *Microtus ochrogaster* and *Peromyscus maniculatus* in sympatry. Trans. Missouri Acad. Sci. 16: 17-23.

Cranford, J. A. (1984) Population ecology and home range utilizations of two subalpine meadow rodents (*Microtus longicaudus* and *Peromyscus maniculatus*). In: Merrit, J. F., ed. Winter ecology of small mammals: v. 10. Spec. Publ. Carnegie Mus. Nat. Hist.; pp. 1-380.

Cronin, K. L.; Bradley, E. L. (1988) The relationship between food intake, body fat and reproductive inhibition in prairie deermice (*Peromyscus maniculatus bairdii*). Comp. Biochem. Physiol. A Comp. Physiol. 89: 669-673.

Deavers, D. R.; Hudson, J. W. (1981) Temperature regulation in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and a shrew (*Blarina brevicauda*) inhabiting the same environment. Physiol. Zool. 54: 94-108.

Dewsbury, D. A.; Baumgardner, D. J.; Evans, R. L.; et al. (1980) Sexual dimorphism for body mass in 13 taxa of muroid rodents under laboratory conditions. J. Mammal. 61: 146-149.

Dice, L. R. (1922) Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. Ecology 3: 29-47.

Drickamer, L. C. (1970) Seed preferences in wild caught *Peromyscus maniculatus bairdii* and *Peromyscus leucopus noveboracensis*. J. Mammal. 51: 191-194.

Drickamer, L. C. (1976) Hypothesis linking food habits and habitat selection in *Peromyscus*. J. Mammal. 57: 763-766.

Drickamer, L. C. (1978) Annual reproduction patterns in populations of two sympatric species of *Peromyscus*. Behavior. Biol. 23: 405-408.

Drickamer, L. C.; Bernstein, J. (1972) Growth in two subspecies of *Peromyscus maniculatus*. J. Mammal. 53: 228-231.

Dunmire, W. W. (1960) An altitudinal survey of reproduction in *Peromyscus maniculatus*. Ecology 41: 174-182.

Eisenberg, J. F. (1981) The mammalian radiations. Chicago, IL: University of Chicago Press.

Fairbairn, D. J. (1977) The spring decline in deer mice: death or dispersal? Can. J. Zool. 55: 84-92.

Fairbairn, D. J. (1978) Dispersal of deer mice, *Peromyscus maniculatus*: proximal causes and effects on fitness. Oecologia 32: 171-193.

Flake, L. D. (1973) Food habits of four species of rodents on a short-grass prairie in Colorado. J. Mammal. 54: 636-647.

Fleharty, E. D.; Krause, M. E.; Stinnett, D. P. (1973) Body composition, energy content, and lipid cycles of four species of rodents. J. Mammal. 54: 426-438.

Fordham, R. A. (1971) Field populations of deermice with supplemental food. Ecology 52: 138-146.

Glazier, D. S. (1979) An energetic and ecological basis for different reproductive rates in five species of *Peromyscus* (mice) [Ph.D. dissertation]. Ithaca, NY: Cornell University.

Green, D. A.; Millar, J. S. (1987) Changes in gut dimensions and capacity of *Peromyscus maniculatus* relative to diet quality and energy needs. Can. J. Zool. 65: 2159-2162.

Gyug, L. W. (1979) Reproductive and developmental adjustments to breeding season length in *Peromyscus* [master's thesis]. London, Ontario: University of Western Ontario.

Gyug, L. W.; Millar, J. S. (1980) Fat levels in a subarctic population of *Peromyscus maniculatus*. Can. J. Zool. 58: 1341-1346.

Halford, D. K. (1987) Density, movement, and transuranic tissue inventory of small mammals at a liquid radioactive waste disposal area. In: Pinder, J. E., III; Alberts, J. J.; McLeod, K. W., et al., eds. Environmental research on actinide elements; November 7-11, 1983; Hilton Head, South Carolina. U.S. Department of Energy, Office of Scientific and Technical Information. Rep. No. CONF-841142 (DE86008713); pp. 147-156.

Halfpenny, J. C. (1980) Reproductive strategies: intra and interspecific comparison within the genus *Peromyscus* [Ph.D. dissertation]. Fort Collins, CO: University of Colorado.

Hamilton, W. J., Jr. (1941) The foods of small forest mammals in eastern United States. J. Mammal. 22: 250-263.

Harris, J. H. (1986) Microhabitat segregation in two desert rodent species: the relation of prey availability to diet. Oecologia (Berl.) 68: 417-421.

Hayward, J. S. (1965) Metabolic rate and its temperature-adaptive significance in six geographic races of *Peromyscus*. Can. J. Zool. 43: 309-323.

Hock, R. J.; Roberts, J. C. (1966) Effect of altitude on oxygen consumption of deer mice: relation of temperature and season. Can. J. Zool. 44: 365-376.

Holbrook, S. J. (1979) Habitat utilization, competitive interactions, and coexistence of three species of cricetine rodents in east-central Arizona. Ecology 60: 758-769.

Howard, W. E. (1949) Dispersal, amount of inbreeding, and longevity of a local population of prairie deer mice on the George Reserve, southern Michigan. Contr. Lab. Vert. Biol., University of Michigan 43:1-52.

Johnson, D. R. (1961) The food habits of rodents in range lands of southern Idaho. Ecology 42: 407-410.

Kantak, G. E. (1983) Behavioral, seed preference, and habitat selection experiments with two sympatric *Peromyscus* species. Am. Midl. Nat. 109: 246-252.

Kaufman, D. W.; Kaufman, G. A. (1989) Population biology. In: Kirkland, G. L.; Lane, J. N., eds. Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech University Press.

King, J. A.; Deshaies, J. C.; Webster, R. (1963) Age of weaning of two subspecies of deer mice. Science 139: 483-484.

Kirkland, G. L.; Lane, J. N., eds. (1989) Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech University Press.

Layne, J. N. (1968) Ontogeny. In: Biology of *Peromyscus* (Rodentia). Spec. Publ., Amer. Soc. Mammal. 2: 1-593.

Linzey, A. V. (1970) Postnatal growth and development of *Peromyscus maniculatus nubiterrae*. J. Mammal. 51: 152-155.

MacMillen, R. E.; Garland, T. J. (1989) Adaptive physiology. In: Kirkland, G. L.; Lane, J. N., eds. Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech University Press.

Marinelli, L.; Millar, J. S. (1989) The ecology of beach-dwelling *Peromyscus maniculatus* on the Pacific coast. Can. J. Zool. 67: 412-417.

Martell, A. M.; MacAuley, A. L. (1981) Food habits of deer mice (*Peromyscus maniculatus*) in northern Ontario. Can. Field Nat. 95: 319-324.

Marten, G. G. (1973) Time patterns of *Peromyscus* activity and their correlations with weather. J. Mammal. 54: 169-188.

May, J. D. (1979) Demographic adjustments to breeding season length in *Peromyscus* [master's thesis]. London, Ontario: University of Western Ontario.

McCabe, T. T.; Blanchard, B. D. (1950) Three species of *Peromyscus*. Santa Barbara, CA: Rood Associates.

McLaren, S. B.; Kirkland, G. L., Jr. (1979) Geographic variation in litter size of small mammals in the central Appalachian region. Proc. Pennsylvania Acad. Sci. 53: 123-126.

McNab, B. K.; Morrison, P. (1963) Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecol. Monogr. 33: 63-82.

Menhusen, B. R. (1963) An investigation on the food habits of four species of rodents in captivity. Trans. Kansas Acad. Sci. 66: 107-112.

Metzgar, L. H. (1973a) Exploratory and feeding home ranges in *Peromyscus*. J. Mammal. 54: 760-763.

Metzgar, L. H. (1973b) Home range shape and activity in *Peromyscus leucopus*. J. Mammal. 54: 383-390.

Metzgar, L. H. (1979) Dispersion patterns in a *Peromyscus* population. J. Mammal. 60: 129-145.

Metzgar, L. H. (1980) Dispersion and numbers in *Peromyscus* populations. Am. Midl. Nat. 103: 26-31.

Meyers, P.; Master, L. L.; Garrett, R. A. (1985) Ambient temperature and rainfall: an effect on sex ratio and litter size. J. Mammal. 66: 289-298.

Millar, J. S. (1975) Tactics of energy partitioning in breeding *Peromyscus*. Can. J. Zool. 53: 967-976.

Millar, J. S. (1978) Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. Ecology 59: 1055-1061.

Millar, J. S. (1979) Energetics of lactation in *Peromyscus maniculatus*. Can. J. Zool. 57: 1015-1019.

Millar, J. S. (1982) Life cycle characteristics of northern *Peromyscus maniculatus borealis*. Can. J. Zool. 60: 510-515.

Millar, J. S. (1985) Life cycle characteristics of *Peromyscus maniculatus nebrascensis*. Can. J. Zool. 63: 1280-1284.

Millar, J. S. (1989) Reproduction and development. In: Kirkland, G. L.; Lane, J. N., eds. Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech University Press; pp. 169-205.

Millar, J. S.; Innes, D. G. (1983) Demographic and life cycle characteristics of montane deer mice. Can. J. Zool. 61: 574-585.

Millar, J. S.; Schieck, J. O. (1986) An annual lipid cycle in a montane population of *Peromyscus maniculatus*. Can. J. Zool. 64: 1981-1985.

Millar, J. S.; Willie, F. B.; Iverson, S. L. (1979) Breeding by *Peromyscus* in seasonal environments. Can. J. Zool. 57: 719-727.

Montgomery, W. I. (1989) *Peromyscus* and *Apodemus*: patterns of similarity in ecological equivalents. In: Kirkland, G. L.; Lane, J. N., eds. Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech University Press; pp. 293-366.

Morris, J. G.; Kendeigh, C. S. (1981) Energetics of the prairie deer mouse *Peromyscus maniculatus bairdii*. Am. Midl. Nat. 105: 368-76.

Morrison, P. R. (1948) Oxygen consumption in several small wild mammals. J. Cell. Comp. Physiol. 31: 69-96.

Morrison, P.; Dieterich, R.; Preston, D. (1977) Body growth in sixteen rodent species and subspecies maintained in laboratory colonies. Physiol. Zool. 50: 294-310.

Murie, M. (1961) Metabolic characteristics of mountain, desert and coastal populations of *Peromyscus*. Ecology 42: 723-740.

Myers, P.; Master, L. L. (1983) Reproduction by *Peromyscus maniculatus*: size and compromise. J. Mammal. 64: 1-18.

Myers, P.; Master, L. L.; Garrett, R. A. (1985) Ambient temperature and rainfall: an effect on sex ratio and litter size in deer mice. J. Mammal. 66: 289-298.

Nagy, K. A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

Nelson, R. J.; Desjardins, C. (1987) Water availability affects reproduction in deer mice. Biol. Reproduc. 37: 257-260.

Reynolds, T. D.; Wakkinen, W. L. (1987) Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho. Am. Midl. Nat. 118: 245-250.

Ribble, D. O.; Samson, F. B. (1987) Microhabitat associations of small mammals in southeastern Colorado, with special emphasis on *Peromyscus* (Rodentia). Southwest. Nat. 32: 291-303.

Rood, J. K. (1966) Observations on the reproduction of *Peromyscus* in captivity. Am. Midl. Nat. 76: 496-503.

Ross, L. G. (1930) A comparative study of daily water-intake among certain taxonomic and geographic groups within the genus *Peromyscus*. Biol. Bull. 59: 326-338.

Sadleir, R. M. (1970) Population dynamics and breeding of the deermouse (*Peromyscus maniculatus*) on Burnaby Mountain, British Columbia. Syesis 3: 67-74.

Schlesinger, W. H.; Potter, G. L. (1974) Lead, copper, and cadmium concentrations in small mammals in the Hubbard Brook Experimental Forest. Oikos 25: 148-152.

Sieg, C. H.; Uresk, D. W.; Hansen, R. M. (1986) Seasonal diets of deer mice on bentonite mine spoils and sagebrush grasslands in southeastern Montana. Northwest Sci. 60: 81-89.

Smith, M. H.; McGinnis, J. T. (1968) Relationships of latitude, altitude and body size to litter size and mean annual production of offspring in *Peromyscus*. Res. Pop. Biol. 10: 115-126.

Stahl, W. R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453-460.

Stebbins, L. L. (1977) Energy requirements during reproduction of *Peromyscus maniculatus*. Can. J. Zool. 55: 1701-1704.

Stebbins, L. L. (1978) Some aspects of overwintering in *Peromyscus maniculatus*. Can. J. Zool. 56: 386-390.

Stebbins, L. L.; Orich, R.; Nagy, J. (1980) Metabolic rates of *Peromsyscus maniculatus* in winter, spring, and summer. Acta. Theriol. 25: 99-104.

Sullivan, T. P. (1979) Repopulation of clear-cut habitat and conifer seed predation by deer mice. J. Wildl. Manage. 43: 861-871.

Svendsen, G. (1964) Comparative reproduction and development in two species of mice in the genus *Peromyscus*. Trans. Kansas Acad. Sci. 67: 527-538.

Svihla, A. (1932) A comparative life history study of the mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., Univ. Michigan 24: 1-39.

Svihla, A. (1934) Development and growth of deermice (*Peromyscus maniculatus artemisiae*). J. Mammal. 15: 99-104.

Svihla, A. (1935) Development and growth of the prairie deer mouse, *Peromyscus maniculatus bairdii*. J. Mammal. 16: 109-115.

Taitt, M. J. (1981) The effect of extra food on small rodents populations: deer mice (*Peromyscus maniculatus*). J. Anim. Ecol. 50: 111-124.

Taitt, M. J. (1985) Cycles and annual fluctuations: *Microtus townsendii* and *Peromyscus maniculatus*. Acta. Zool. Fenn. 173: 41-42.

Tannenbaum, M. G.; Pivorun, E. B. (1988) Seasonal study of daily torpor in southeastern *Peromyscus maniculatus* and *Peromyscus leucopus* from mountains and foothills. Physiol. Zool. 61: 10-16.

Tannenbaum, M. G.; Pivorun, E. B. (1989) Summer torpor in montane *Peromyscus maniculatus*. Am. Midl. Nat. 121: 194-197.

Thomas, B. (1971) Evolutionary relationships among *Peromyscus* from the Georgia Strait, Gordon, Goletas, and Scott Islands of British Columbia, Canada [Ph.D. dissertation]. Vancouver, BC: University of British Columbia.

Tomasi, T. E. (1985) Basal metabolic rates and thermoregulatory abilities in four small mammals. Can. J. Zool. 63: 2534-2537.

van Horne, B. (1982) Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63: 992-1003.

Vaughn, T. A. (1974) Resource allocation in some sympatric subalpine rodents. J. Mammal. 55: 764-795.

Vickery, W. L. (1981) Habitat use by northeastern forest rodents. Am. Midl. Nat. 106: 111-118.

Whitaker, J. O., Jr. (1966) Food of *Mus musculus*, *Peromyscus maniculatus bairdi*, and *Peromyscus leucopus* in Vigo County, Indiana. J. Mammal. 47: 473-486.

Wolff, J. O. (1985a) The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. Can. J. Zool. 63: 2657-2662.

Wolff, J. O. (1985b) Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. Can. J. Zool. 63: 1548-1555.

Wolff, J. O. (1986) The effects of food on midsummer demography of white-footed mice, *Peromyscus leucopus*. Can. J. Zool. 64: 855-858.

Wolff, J. O. (1989) Social behavior. In: Kirkland, G. L.; Lane, J. N., eds. Advances in the study of *Peromyscus* (Rodentia). Lubbock, TX: Texas Tech. University Press; pp. 271-291.

Wolff, J. O.; Durr, D. S. (1986) Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. J. Mammal. 67: 409-412.

Wolff, J. O.; Hurlbutt, B. (1982) Day refuges of *Peromyscus leucopus* and *Peromyscus maniculatus*. J. Mammal. 63: 666-668.

Wolff, J. O.; Freeberg, H.; Dueser, R. D. (1983) Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). Behav. Ecol. Sociobiol. 12: 237-242.

Wolff, J. O.; Dueser, R. D.; Berry, D. S. (1985) Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. J. Mammal. 66: 795-798.

Zegers, D. A.; Merritt, J. F. (1987) Seasonal changes in non-shivering thermogenesis of three small mammals (abstract only). Bull. Ecol. Soc. Am. 68: 455.

Zegers, D. A.; Merritt, J. F. (1988) Adaptations of *Peromyscus* for winter survival in an Appalachian montane forest. J. Mammal. 69: 516-523.